Adaptive Behavior and the Function of Working Memory

Kumulative Habilitationsschrift
zur Erlangung der *Venia legendi*
an der Mathematisch-Naturwissenschaftlichen Fakultät
der Eberhardt-Karls-Universität Tübingen

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Tübingen, im Dezember 2014

meinen Eltern

Reinhard und Karin Hardieß

List of contents

1 Alphabetical list of articles submitted for validation of the written part of the habilitation.

Own contribution to articles with co-authorship will be explained in detail for each article.

1. Hardiess G., Basten K. & Mallot H.A. (2011). Acquisition vs. memorization trade-offs are modulated by walking distance and pattern complexity in a large-scale copying paradigm. *PLoS ONE*. 6(4):e18494, doi:10.1371/journal.pone.0018494.

   Together with KB, I conceived and implemented the experiments. I performed the experiments. Together with KB, I analyzed the data and together with HAM, I wrote the manuscript. I carried out the literature search.

2. Hardiess G., Halfmann M., Hamm F. & Mallot H.A. (submitted). Flexible spatial representation is supported by explicit place labeling in survey, but not in route learning. *Psychological Science*.

   Together with FH and HAM, I conceived and designed the experiments. Together with MH, I performed the experiments, analyzed and interpreted the data. Together with HAM, I wrote the manuscript. I carried out the literature search.

3. Hardiess G., Hansmann-Roth S. & Mallot H.A. (2013). Gaze movements and spatial working memory in collision avoidance: a traffic intersection task. *Frontiers in Behavioral Neuroscience*. 7(62), 1-13, doi:10.3389/fnbeh.2013.00062.

   Together with SHR, I conceived and implemented the experiment. Together with SHR, I performed the studies. Together with SHR, I analyzed the data and HAM and me, we wrote the manuscript. I carried out the literature search.

4. Hardiess G. & Mallot H.A. (under revision). Allocation of cognitive resources in comparative visual search - individual and task dependent effects. *Vision Research*.

   I designed, implemented, and performed the experiments and analyzed the data. Together with HAM, I wrote the manuscript. I carried out the literature search.

5. Hardiess G. & Mallot H.A. (2010). Task-dependent representation of moving objects within working memory in obstacle avoidance. *Strabismus*. 18(3), 78-82, doi:10.3109/09273972.2010.502958.

   I conceived and implemented all experiments, performed the studies, and analyzed the data. Together with HAM, I wrote the manuscript. I carried out the literature search.

6. Hardiess G., Papageorgiou E., Schiefer U. & Mallot H.A. (2010). Functional compensation of visual field deficits in hemianopic patients under the influence of different task demands. *Vision Research*. 50(12), 1158-1172, doi:10.1016/j.visres .2010.04.004.[1]

   I conceived and implemented the experiments. Together with EP, I performed the study. Together with HAM and EP, I analyzed the data. HAM, EP, US, and me, we wrote the manuscript. I carried out the literature search.

7. Papageorgiou E., Hardiess G., Ackermann H., Wiethoelter H., Dietz K., Mallot H.A. & Schiefer U. (2012). Collision avoidance in persons with homonymous visual field defects under virtual reality conditions. *Vision Research*. 52(1), 20-30, doi:10.1016/ j.visres.2011.10.019.

   I conceived and implemented the experiment. EP and US recruited the patients. Together with EP, I performed the study. Together with EP, HA, HW, and KD, I analyzed the data. EP and me, we wrote the manuscript. I carried out the literature search.

8. Papageorgiou E., Hardiess G., Mallot H.A. & Schiefer U. (2012). Gaze patterns predicting successful collision avoidance in patients with homonymous visual field defects. *Vision Research*. 65, 25-37, doi:10.1016/j.visres.2012.06.004.

   I conceived and implemented the experiment. EP and US recruited the patients. Together with EP, I performed the study. Together with EP, I analyzed the data. EP, HAM and me, we wrote the manuscript. I carried out the literature search.

9. Papageorgiou E., Hardiess G., Wiethoelter H., Ackermann H., Dietz K., Mallot H.A. & Schiefer U. (2012). The neural correlates of impaired collision avoidance in hemianopic patients. *Acta Ophthalmologica*. 90(3): e198-205, doi:10.1111/j.1755-3768.2011.02315.x.

   I conceived and implemented the experiment. EP and US recruited the patients. Together with EP, I performed the study. EP, HW, HA, and KD analyzed the data. EP, US, and me, we wrote the manuscript. I carried out the literature search.

10. Röhrich W.G., Hardiess G. & Mallot H.A. (2014). View-based organization and interplay of spatial working and long-term memories. *PLoS ONE.* 9(11): e112793, doi:10.1371/journal.pone.0112793.

    Together with WR and HAM, I designed and implemented the experiments. WR performed the study. WR, HAM, and me analyzed the data and wrote the manuscript. Together with WR, I carried out the literature search.

[1] parts of this article were already used in the doctoral thesis

2 Acknowledgements

The studies summarized in this thesis are obviously not the work of a single person and could hardly be accomplished only by myself. Indeed, several colleagues and students contributed to the research that I performed in the last couple of years.

First of all, I am very grateful to Prof. Dr. Hanspeter A. Mallot for his deep and continuous support, for countless inspiring discussions and for sharing his tremendous knowledge about so many scientific topics and methodological issues. I fully enjoyed the atmosphere in his Lab of Cognitive Neuroscience at the Institute of Neurobiology and it was a pleasure to work with Dr. Hansjürgen Dahmen, Dr. Sabine Gillner, Dr. Jan Wiener, Dr. Christian Hölscher, and all the other former and actual colleagues and students.

I especially want to thank my parents for their continuous support and their absolute confidence in me during all those years of my student, PhD student, and post-doc time.

3 Introduction

» Our brains are minuscule fragments of the universe, much too small to hold all the facts of the world but not too idle to speculate about them. «

Valentino Braitenberg, Vehicles: Experiments in Synthetic Psychology

In animals, the fundamental basis for the interaction with the environment and, in the end, for the generation of adaptive behavior is the sensory-motor cycle (also known as action-perception loop) as already described in the 1920s by Jakob von Uexküll (see figure 1A). Processing this cycle, external information from the environment is perceived by the sensors of the animal, processed and interpreted by neuronal circuits, and is finally responded to with the generation of adequate motor behavior to interact with the world. By utilizing this action-perception loop, animals modify the outer world as well as their own perception of the environment.

Successful survival depends on effective measurement, evaluation, and integration of information from the external environment to form internal representations (i.e., theories about nature). As well as the handling of external factors, the knowledge and controlling of internal states must be considered. Dependent on the phylogenetic and ontogenetic level of an animal as well as on the task at hand, the handling of information in an action-perception loop can involve neuronal processing from a low up to a high amount of stages (see figure 1B). In higher animals, one should not assume just one pathway (going up to the highest regions of sensory processing, further to prefrontal regions, and down to motor output). From neuroanatomical findings about the brain, it could be reasoned that there are numerous pathways (cortical streams) from most intermediate levels of the sensory system to intermediate frontal regions (Distler et al., 1993). Furthermore, it seems that the brain uses the most appropriate of such pathways and regions to solve the task at hand.

Behavior lacking flexibility is found when just stereotyped input-output relations exist, i.e. the incoming sensory information is directly and rigidly connected with motor functions. On the other end, the highest processing flexibility provides the ground for adaptive behavior and can be obtained when cognition is involved. Here, spatio-temporal processing supported by memory functions (representation networks) is capable to generate complex and adaptive behavior (Baddeley, 1992; Wood et al., 2012). Representation networks are developed by experience and organize themselves hierarchically by order of complexity or abstraction of their content (see figure 1C). All cognitive, adaptive functions consist of transactions within and between such neural networks. The networks range from simple sensory and motor ones, located near primary sensory and motor areas, to complex ones (located in the higher cortical association areas), where categorical knowledge is derived from multiple instantiations (Fuster, 2008).

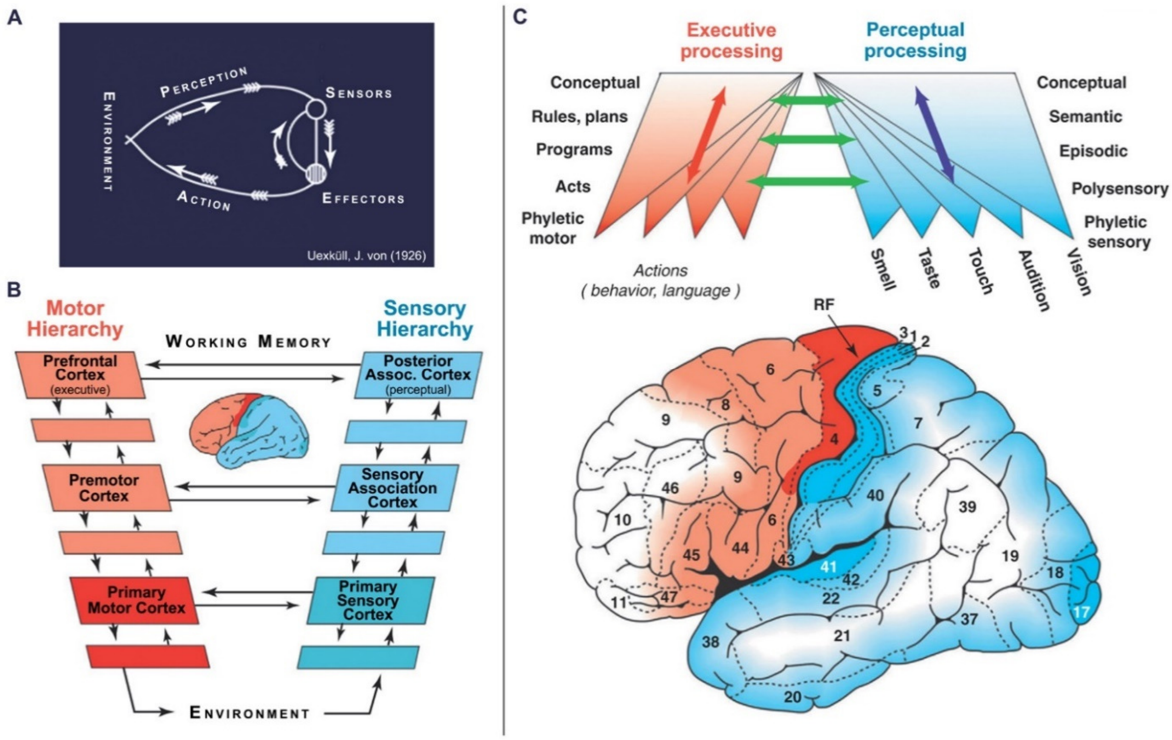

Figure 1. Neuronal information processing. A) Basic diagram of the sensory-motor cycle from Von Uexküll with the internal nervous feedback from efferents to sensors. B) Connections between cortical regions involved in the action-perception cycle. Unlabeled parts of the cycle denote intermediate areas or subareas of the labeled regions. Connections between the two hierarchies occur at several levels, not just at the top level. C) Schematic diagram of the perceptual and executive processing hierarchies of memory. Perceptual networks are organized hierarchically between primary sensory areas (blue) and posterior association cortex (white) by order of category of perceptual memory, from phyletic sensory memory (sensory cortex) at the bottom to conceptual perceptual knowledge at the top. Executive networks are organized hierarchically between primary motor cortex (red) and prefrontal cortex (white) by order of category of executive memories, from phyletic motor memory (motor cortex) at the bottom to conceptual executive knowledge at the top. Overlapping triangles with vertex down symbolize the neural substrate for upward expanding and interconnected networks. Cortico-cortical connectivity exists between different hierarchical levels of memory (blue and red arrows) and between perceptual and executive hierarchies (green arrows). In the lateral view of the left hemisphere, brain areas were numbered according to Brodmann's cytoarchitectonic map (RF: Rolandic fissure). (modified after Fuster & Bressler, 2012 and Von Uexküll, 1926).

In human beings, the highest level of information processing is realized through the interplay between cognitive core domains such as perception, control of action, attention, executive function, learning and the memory system. The latter one, memory, is generally discussed as a system enabling the storage of information acquired from agent–environment interactions and the subsequent recall in the service of behavior. Functionally, memory processes can be divided into three distinct operations: encoding, storage (maintenance), and retrieval (recall) of information. Conceptually and according to temporal as well as capacity considerations, the memory system is subdivided in and composed of three inter-connected memory modules: the sensory, the working (short-term), and the long-term memory (Hebb, 1949). Sensory memory is the ultra-short-term store, where information (taken in by sensory receptors) is retained less than a second but long enough to be transferred to short-term memory. In the visual domain such a sensory store is termed as iconic memory (Coltheart, 1980). Short-term or working memory is the memory system that temporarily stores information in the service of an ongoing task (Cowan, 1999) and will be explained in more detail in section 3.2. Long-term memory is the subsystem where data can be stored for long periods of time. Here, non-conscious, procedural (or implicit) memory underpinning skilled behavior, habits, and conditioning, is differentiated from consciously accessible, declarative (or explicit) memory for facts and information (Cohen & Squire, 1980; Graf & Schacter, 1984).

3.1 Adaptive behavior

Adaptive behavior is the ability and advantage of an organism to behave adequately and to react flexibly to changing environmental conditions in order to increase the own fitness to survive in the wild. Thus, the organism can modify an unconstructive or disruptive behavior to something more constructive to meet the demands of everyday living. And as Simon mentioned: "The human mind is an adaptive system. […] Moreover, it can store new knowledge and skills that will help it attain its goals more effectively tomorrow than yesterday: It can learn. As a consequence of the mind's capacities for adaptation and learning, human behavior is highly flexible and variable, altered by both circumstances and experience." (Simon, 1992: p. 15).

In classical theories, the brain was considered as a passive, stimulus-driven processor that simply reacts to sensory inputs by the sequential extraction and recombination of the stimulus features, i.e., bottom-up processing in hierarchically organized neural architectures (Aloimonos & Rosenfeld, 1991; Biederman, 1987; Thorpe et al., 1996). Thus, the internal model of the world was believed to provide just context-invariant knowledge about the external environment (Engel et al., 2001). In recent times, new data favor the view of the brain as a much more active, flexible, and adaptive system with intimate relationships between action and cognition (Churchland et al., 1994; Clark, 1999; Fahle, 2009), realized through real-world interactions of the brain and the dynamics of neuronal networks (Beer, 2000; Singer & Gray, 1995). Without doubt, the topmost goal for cognition is the generation and guidance of adequate actions. Thus, cognitive operations need not contain 'correct' representations of the world's features, but should provide the generation of actions that are optimally adapted to the particular task and repertoire of the organism, a concept termed as 'situatedness' or 'embodied cognition' (Varela et al., 1991). Using top-down mechanisms, predictions about forthcoming stimuli become possible (Ernst & Bülthoff, 2004; Wolfe & Cave, 1999), which are then continuously matched against signals from the outside (environment) and the inside (body). In the process of applying top-down mechanisms on incoming stimuli, the prefrontal and parietal cortex seem to play an important role (Frith & Dolan, 1997; Miller & Cohen, 2001). Cross-systems interactions between prefrontal and parietal areas were identified (Fuster, 2008; Miller, 2000) where assemblies of neurons that represent action goals in the prefrontal cortex modulate sensorimotor circuits that have to carry out response selection.

In conclusion, intelligent and adaptive behavior presupposes that cognition can emancipate itself to varying degrees from the current stimulus situation, and select - considering intrinsic constraints, needs, goals, and motivational states - only those inputs that are meaningful for the control of action. Here, fast and reliable computations became possible by the efficient use of top-down processes, providing predictions for and matching expectations against signals from the environment (Schall, 2001). Furthermore, learning, attention, working memory, stimulus familiarity, and the behavioral context must be considered as top–down factors capable to modulate such signal processing (Fahle, 2009).

3.2 Gaze movements - Acquisition of external information

Since Yarbus has shown in 1967 that spatio-temporal patterns of human eye positions depend strongly on internal goals, gaze movements (i.e., combined eye and head movements; cf. figure 2B) were seen as a window into the attentive mind. More precisely, top-down and attention driven motor outputs were generated to select the most informative parts of the external environment to capture its most important and appropriate (in terms of the current task) piece by guiding the gaze (overt attention). Here, the function of attention to the process of vision introduces selectivity (Treisman, 1996), i.e., the information channel is selectively open for a certain location, time, stimulus dimension, or a combination thereof, but (nearly) closed for all others (Driver, 2001). Note that besides overt attention the concept of covert attention (attention not correlated with gaze position; Carrasco, 2011) exists but will not be considered further in this thesis.

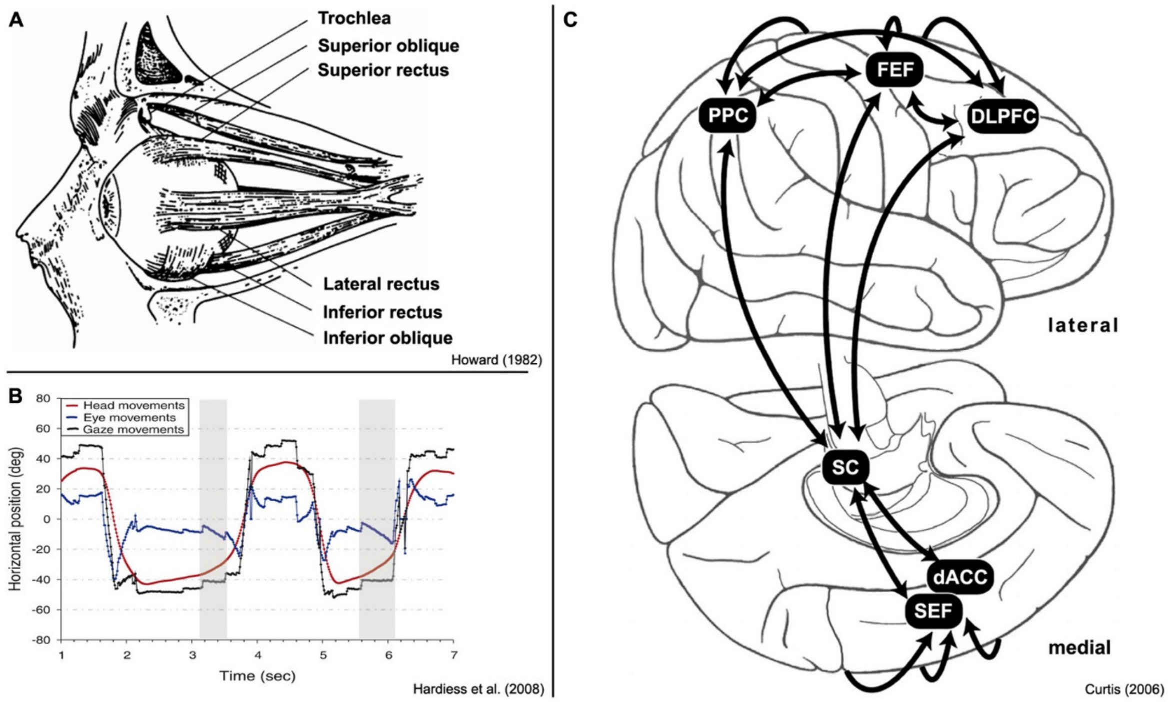

Figure 2. Eye movements and oculomotor pathway. A) Schematic drawing of the eye and the six oculomotor muscles allowing three degrees of freedom movements. B) Exemplary recording of horizontal eye (blue), head (red), and gaze (black) movements during visual search. Note that under moving head conditions, target fixation amounts to compensatory movements of the eyes relative to the head under control of the vestibular-ocular reflex (grey areas). C) Connections between the nodes (SC - superior colliculus, dACC - dorsal anterior cingulate cortex, DLPFC - dorsal lateral prefrontal cortex, FEF - frontal eye field, PPC - posterior parietal cortex, SEF - supplementary eye fields) of the oculomotor network in the human brain. This network, with the SC serving as the final common pathway, is thought to govern the generation of saccades.

Techniques to measure objectively and quantify eye movements are numerous. In principle, three general recording techniques are currently used: EOG (electrooculography; measuring of the corneo-retinal standing potential of the eye), inductive sensors (search coil; measuring of the variation of the magnetic flux of a coil that adheres to the eye), and imaging based tracking (cornea reflex and/or pupil tracking by using infrared light sensitive video cameras). In the field of psychophysics, image based systems were preferred. Such systems can be mounted on the head and allow the participant to move the head freely while wearing the tracker during everyday situations (i.e., experiments are not restricted to computer screens).

Eye movements are highly frequent and occur on average approximately three times per second. Caused by the varying spatial resolution of the retina (determined by the distribution of the photoreceptors) with just one small region of highest resolution (the fovea, located in the center of the macula region), the eyes must be constantly moved to shift the fovea towards informative parts of the environment, i.e., foveal vision is required for activities where highly detailed visual information is of primary importance. The oculomotor network (figure 2C; see also Acs & Greenlee, 2008; Raabe et al., 2013) was identified for the generation of eye movements which were executed through the control of six oculomotor muscles (see figure 2A). In general, eye activities were divided in fixational and saccadic movements (see Kowler, 2011). The main function of fixational movements is the stabilization of a certain attended section (of the outer world) on the foveal region of the eyes (Martinez-Conde, 2004). Without such a stabilization ranging from milliseconds (in case of a stable environment) to seconds (in case of moving objects tracked by smooth pursuit movements), the visual system would hardly be able to extract the external information needed to fulfill the task at hand. Saccadic movements were needed to reorient the eyes (i.e., the line of sight) rapidly towards new sections of the scenery. These movements were characterized as jerky and salutatory activities where the eyes move unconsciously as fast as they can (Carpenter, 1988). Besides the voluntary eye activities discussed so far, others, rather involuntary and micro-movements, were found (e.g., microsaccades, tremor, drift) but are not debated in this thesis.

3.3 Working memory - Internal representation of information

In the field of cognitive science, there exists a long-lasting and ongoing debate about the concept and the function of working memory (Miyake & Shah, 1999). Thirty years ago, Baddeley & Hitch (1974) introduced their highly influential cognitive, multi-component model of working memory where multiple and distinct components or modules (supporting executive control as well as active maintenance of temporarily maintained information) were supposed. This model was later extended by the episodic buffer, capable of multi-dimensional coding and allowing for information binding to form an integrated episode (Baddeley, 2000). Another cognitive model, presented by Cowan (1988, 1999), did not propose dedicated storage buffers but rather embedded processes, capable to integrate activated long-term, short-term, or working memories spotlighted by the focus of attention at a given time (cf. also Anderson, 1983). Here, working memory is not so much determined in size or region as by the level of activation (higher or lower) of relevant representations and by the discriminability of activation levels between relevant and irrelevant representations.

In recent times, working memory is considered rather as an active memory, i.e., memory in active state, which the agent needs for the performance of acts in the short-term (Fuster, 2008). More precisely, working memory refers to the temporary retention of information (visual, auditory, motor, etc.) that was just experienced (external information) or just retrieved from long-term memory (internal information) but no longer exists in the external environment. These memory representations are short-lived but can be stored for longer periods of time through active maintenance or rehearsal strategies, and they can be subjected to various operations that manipulate the information in such a way that makes it useful for goal-directed, adaptive behavior.

Anatomically, functional working memory is achieved through a distributed network of brain regions, where the prefrontal cortex (PFC) as control structure (dorsal prefers active, ventral passive tasks) is critical for the processing of memory operations and the active maintenance of internal representations (Curtis & D'Esposito, 2003; Curtis, 2006). PFC is connected (through feedforward and feedback connections) with the sensorimotor cortical areas enabling a dynamic interplay between them (see figure 1B and C). Thus, working memory is not localized to a single brain region but is an emergent property of the functional interactions between the PFC and the rest of the brain (Pasternak & Greenlee, 2005).

Regarding storage capacity, visual working memory processes information of approximately three to five items at a time, coded as integrated object representations rather than as a collection of separated visual features (Alvarez & Cavanagh, 2004; Vogel et al., 2001). Here, working memory capacity limitations are discussed in two lines of theories. The 'fixed-resource theory' (Zhang & Luck, 2001) conceptualizes working memory as limited-capacity channel with a fixed number of three to four slots over which observers can flexibly allocate information with fixed precision. In this view, a complex item (object) will allocate more slots for retention than a simple one. The other class of theories ('flexible-resource') claims that working memory capacity is limited by the availability of processing resources (Bays & Husain, 2008; Luck & Vogel, 2013). Here, the maintenance of an item requires some amount of cognitive effort and applying this effort depletes the resource pool. As a consequence, an observer can either maintain a low amount of precisely-represented or a higher amount of less-precisely encoded items before resources run out (Franconeri et al., 2013).

4 Research topics and key findings

4.1 Part 1: Compensatory behavior - Gaze strategies in hemanopic patients

relevant articles: publication #6, publication #7, publication #8, publication #9

Gaze (eye + head) movements together with attentional shifts are key elements of visual behavior where gaze patterns will depend on several factors including the size and layout of the visual field, central visual processing capacities, working and long-term memory, and the specific task demands.

If one complete half or parts of the visual field are lost (i.e., scotomas), the visual functions responsible for the control of gaze movements and hence for the collection of external information must adapt. Here, studies with patients suffering from visual field deficits are instrumental in assessing the gaze strategies and their adaptation to reduced information intake and maybe reduced processing capacities. Such an abrupt and severe reduction of the functional size of the visual field appears in patients with homonymous visual field defects (HVFDs). Such patients are impaired by a restricted visual field due to scotomas caused by unilateral post-chiasmal brain damage (Zihl, 1994) because of cerebrovascular accident, traumatic brain injury, or tumors (e.g. Kerkhoff, 1999; Zihl, 2000). As mentioned before, the visual field of HVFD patients lacks up to one complete hemifield (with or without macular sparing) in the case of complete homonymous hemianopia. Such impairments commonly lead to reading difficulties (Schuett et al., 2008) and problems in obstacle avoidance, i.e., patients cannot comprehend an entire visual scene at a glance (Goodwin, 2014).

In order to access the degree of a given impairment in HVFD patients and consequently, to evaluate them concerning driving abilities and other everyday life activities (Gall et al., 2009; Martin et al., 2007; Papageorgiou et al., 2007), the extent of the remaining and intact visual field is measured by static or dynamic perimetry (Papageorgiou et al., 2007). However, it seems that HVFD patients with similar visual field defects, as assessed by perimetry, show different degrees in their functional compensation and behavioral performance (**publication #6, #7, and #8**). Moreover, the performance of some patients was in the range of normal subjects. Interestingly, demographic parameters as age, gender, and time since brain lesion were found as less predictive concerning task performance (**publication #7**). Also no performance differences were revealed between patients with right- and left-hemispheric lesions (**publication #9**). Consequently, additional research was needed in order to investigate the functional compensation behavior of HVFD patients under different task constraints, i.e., measuring of gaze strategies and task performance in experiments demanding the visual system differently. Therefore, I developed and performed three different visual exploration tasks, i.e., dot counting (**publication #6**), comparative visual search (**publication #6**), and collision avoidance in driving (**publication #7, #8, and #9**), with differing demands on visual and cognitive functions. Furthermore, I used virtual reality combined with eye and head tracking techniques while stimulating the entire visual field and assessed vision as well as performance related parameters in unimpaired subjects and HVFD patients. Using MRI (magnetic resonance imaging), the brain site and exact extent of the lesion was assessed in all patients by the eye hospital of Tübingen.

Interestingly, at least half of all tested HVFD patients showed performance values comparable with that of the health group (**publication #6 and 8**) and were classified and labeled as adequate ($HVFD_A$). The remaining pool of patients with poor performance values was labeled as inadequate ($HVFD_I$). Here, the degree of adequacy was not a function of the task but rather determined by the competence of the participant. In order to investigate the determinants, gaze patterns and lesion characteristics were analyzed. In the simplest dot counting task, results in agreement with previous studies (Tant et al., 2002; Zihl, 1995, 1999) were obtained: the gaze pattern of $HVFD_A$ patients and normal controls did not differ significantly with respect to any of the investigated gaze parameters. But, $HVFD_I$ patients showed increased gaze parameters, including number of fixations, proportion of fixations to the side of HVFD, scanpath length, and repetition of fixations (**publication #6**). In contrast, for the cognitively more demanding comparative visual search paradigm, a striking different pattern of compensatory strategy use was found. Adequately performing patients now changed to increased gaze activity that allowed dealing with the higher task demands. Compared to controls, $HVFD_A$ showed an increased number of fixations and scanpath length, while the mean amplitude of saccades was decreased. For this group of patients, we suggested the potential to rely more strongly on visuo-spatial working memory (to guide memory saccades; Aivar et al., 2005) to compensate for the limited information intake due to the impaired visual field (to guide saccade targeting). In the most cognitively challenging collision avoidance task (under dynamic and time-constrained conditions), $HVFD_A$ patients also invested increased gaze scanning, including more fixations on vehicles and fewer fixations on the intersection than $HVFD_I$ patients, leading to successful collision avoidance (**publication #8**). The increased scanpath length, number of gaze shifts and especially the number of fixations on vehicles and mean gaze eccentricity reveals for a compensation by means of exploratory gaze movements in $HVFD_A$ patients.

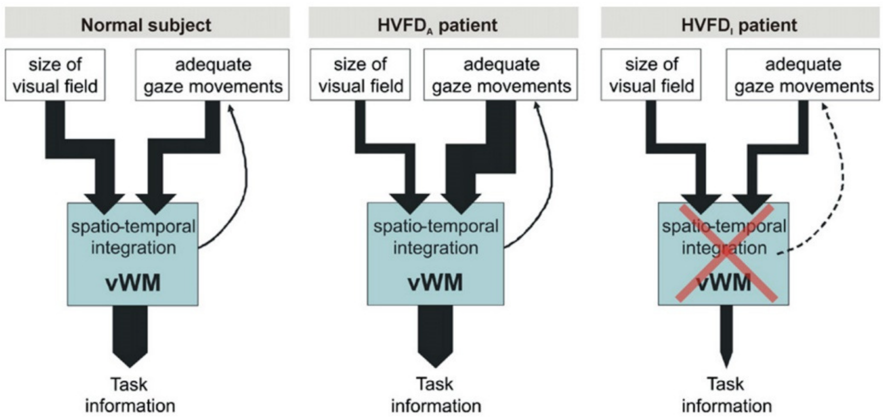

Figure 3. A proposed model for compensatory strategies of normal subjects, $HVFD_A$ patients, and $HVFD_I$ patients under dynamic, virtual reality environments. The usable size of the visual field, the adequacy to uptake visual information from the environment, and the possibility to integrate information in working memory determine task performance (**publication #8**).

Based on brain lesion measurements (**publication #6 and 9**) and in agreement with other authors (Martin et al., 2007), we argued for a working memory component, which can be used only insufficiently in $HVFD_I$ patients, but is more intensified engaged in $HVFD_A$ patients (see figure 3). Furthermore, in combination with intact working memory, gaze adaptation is the primary compensatory mechanism to achieve adequate performance levels in dynamic and cognitively challenging tasks. Lesion analyses showed clear differences concerning the affected regions in $HVFD_A$ and $HVFD_I$ patients (**publication #9**). Right-hemispheric damage was more frequent in $HVFD_A$ in the parieto-occipital region and the posterior cingulate gyrus. In $HVFD_I$ patients, left-hemispheric damage was more likely to involve the inferior occipital cortex and the fusiform (occipito-temporal) gyrus. Regarding the site of brain lesion, our results are consistent with a recent study on hemianopes in visual search (Machner et al., 2009). They found that the mesio-ventral areas of the temporal lobe were damaged in at least half of the severely impaired patients but spared in the mildly impaired patients. Consequently, processes of visual object recognition, including color, texture, and form information and the control of attention may be affected in $HVFD_I$ patients. In addition, any damage of the para-hippocampal gyrus (input–output pathway between the hippocampus and cortical association areas) would lead to cognitive deficits including decline in memory storage or retrieval from other brain areas.

In conclusion, the investigations about the compensation strategies in hemianopics showed clearly that clinical as well as demographic parameters (size and lateralization of the scotoma, age, gender, time since brain lesion, etc.) seemed to be less predictive concerning task performance (see also Kasneci et al., 2014). Instead, and dependent on task demands, adequate gaze movements to compensate for the visual field loss (cf. Bowers et al., 2014) together with an intact visual-spatial working memory (Hardiess et al., 2013) must be considered when the functional compensation behavior of hemianopic patients is evaluated.

4.2 Part 2: Gaze behavior and working memory - Collision detection

relevant articles: publication #3, publication #5

Dynamic and multi-object collision detection and obstacle avoidance in street crossing is an everyday activity human beings perform without any effort. However, such activities are highly demanding concerning the extraction, selection, and representation of spatio-temporal information of all the relevant obstacles in an optimized format. For simple interceptive actions, bottom-up processing of the optical (or retinal) flow (Lappe et al., 1999; Fajen, 2005) in order to perceive the time-to-contact (Lee, 1976) or time-to-passage (Kaiser & Mowafy, 1993) is obviously required. As example, an object's time-to-collision can easily be calculated as the ratio of the object's image size on the retina to the rate of change of this size (a ratio termed as *tau*, Lee, 1976). Despite the huge amount of findings, showing that simple visual calculations like *tau*, *tau*-related function, object bearing (i.e., the angle between the heading and an intercepting object) and others can in principle be used to obtain an estimate of the potential-of-collision (POC) of an object, the neuro-scientific evidence for such principles is quite small (Frost, 2010; Zago et al., 2009). Nevertheless, bottom-up processed visuo-motor control without awareness (pre-attentively) is probably the normal mode regarding fast and skilled interceptive actions, but top-down (cognitive) processes (i.e., prior knowledge, gaze shifts, predictions, attention, and working memory) must be assumed when complex, multiple-object, and dynamic tasks were presented (Andersen & Kim, 2001; Franconeri et al., 2013; Hayhoe et al., 2012; Jovancevic et al., 2006; López-Moliner et al., 2007).

In order to show the contribution of gaze shifts, attention, and working memory to the process of estimating the potential-of-collision (POC) regarding a variety of moving objects, I designed and accomplished a series of street crossing experiments in virtual reality while measuring gaze movement (**publication #3 and 5**). In principle, the street crossing paradigm confronted participants always with an approach to a two-lane intersection and with the task to detect and avoid potential collisions. In some situations (trials), participants had active control over their own speed (by the mean of a joystick) and needed to cross the intersection interactively without causing a crash (i.e., to find the free space for crossing). In other conditions, participants were challenged to monitor the intersection while passively approaching the intersection in order to test their memory representation of the traffic scenery in later recall (**publication #5**). With these conducted experiments I was able to provide a new perspective of the role of gaze behavior and spatial memory in collision detection and avoidance answering the following questions: How do gaze movements and working memory contribute to collision avoidance when multiple moving objects are present and how do they correlate with task performance?

The overall gaze pattern was determined by an initial left-right-left shift occurring in most of the participants. This pattern was assumingly due to a well-trained and habituated gaze behavior on streets with right-hand traffic. Interestingly, local oscillations (overlaid to the left-right-left pattern) also occurred, allowing to sample and select the most relevant cars regarding their POC (**publication #3**). These oscillations were interpreted as a global gaze strategy. In addition to such global adaptations, two task-specific properties of the gaze behavior could be identified. First, only cars moving toward the intersection are taken into consideration, i.e., cars that have already passed the intersection point were ignored. Clearly, 'inward' driving cars have the higher POC and attracted attention. Second, the allocation of attention (i.e., distribution of fixations) during the approach to the intersection was scaled by the participant's distance to the intersection. Here, gaze amplitudes were found as the highest with low allocation of attention when the distance to the intersection was large. The further a participant approached, the more often smaller gaze amplitudes and higher attentional levels were found (**publication #3**). Consequently, attention can be allocated broadly and with low intensity in the early stage of the approach, because the actual POC is relatively small as long as the intersection is distant. The allocation peaks more and more and ends up as a localized, high amplitude peak where the relevant time window is very small and POC considerations concern only one single position of possible colliding cars. Such a pattern of gaze movements should be expected, since attentional and thus working memory resources are fixed and limited. Quantitative investigations about memory representations regarding a certain approach distance were also performed using scene re-constructing (**publication #5**) and change detection tasks (**publication #3**). Here, cars driving to the right were mostly placed left of the intersection while cars driving to the left were placed predominantly on the right side, i.e., high POC cars were remembered and recalled better than cars with low POC.

In conclusion, regardless of task performance (i.e., prediction of a collision event) gaze patterns were found as very similar and less predictive. The majority of gaze movements could be accounted for by global gaze shifts out of habits (on intersections) and strategies to select only cars with a significant and high POC (as a function of approaching distance; see also **publication #8**). Finally, during the representation within working memory, cars were evaluated and weighted based on their POC. In consequence, the high variability concerning task performance found in the whole population of participants could not, or only to a minor degree, be related to gaze behavior. Rather, participants must differ in the mental processes of representing the equally selected material within spatial memory. Such mental processing must be attributed to executive functioning, capacity and capability of working memory, learning abilities, anticipation, or internal models (Zhao & Warren, 2014). Here, individual differences have to be assessed independently of the primary visual task and should be helpful when predicting collision detection performance in dynamic, multiple object tracking tasks.

4.3 Part 3: Decision behavior - Trade-offs between working memory and visuo-motor strategies

relevant articles: publication #1, publication #4

Nearly every human activity consists of a mixture of cognitive, perceptual, and motor processes as depicted in figure 1. And the majority of human behaviors is considered as complex. Complexity arises, since the high organization, connectivity, and dynamic interactions of brain structures that lead to cognition enable the completion of tasks in a manifold manner. Here, decisions became necessary, able to select the most adequate, convenient, or optimal performance that allows the highest or an optimal behavioral gain.

As one of the fundamental decision models used in economics and marketing, the 'rational model' was introduced (Simon, 1955). However, such a model was rarely tested as satisfying in psychology, since it assumes that decision makers must necessarily have access to all relevant information in their decision environment, and that information integration should not be influenced by external or internal factors. By introducing cognitive capacity and processing limitations into the decision process, Simon (1957) described the 'bounded rationality model'. Here, the assumption of the rational models concerning the use of full and relevant information must be scrapped, since choice environments mostly contain material that exceed the cognitive processing capacity. Consequently, decisions were made by prioritizing the information to which to attend. Thus, by selecting a decision strategy or 'heuristic', the process of decision could be shortened (e.g., Gigerenzer & Gaissmaier, 2011). Several different heuristics have been proposed (e.g., elimination by aspect, take the best, recognition heuristic, etc.) and have been shown to outperform the rational models. The most important commonality between all kinds of heuristics is that decision makers need a mental representation of the choice problem, and that a heuristic is chosen based on a meta-cognitive strategy selection rule. In recent times, other decision models were proposed (e.g., attentional drift diffusion model, Decision Field Theory, parallel constraint satisfaction model; see Orquin & Loose, 2013), but not further explained in this thesis.

Contrarily to the eye-mind assumption (i.e., theory about a strong causal relationship between working memory, attention, and oculomotor behavior; e.g. Just & Carpenter, 1976), in recent studies about problem solving and decision making it was found that participants often rely on eye movements to use the environment as an external memory space, thereby reducing demands on working memory (e.g., Droll & Hayhoe, 2007; Hardiess et al., 2008; Karn & Hayhoe, 2000). In its extreme use, this strategy was termed as 'just-in-time', where information from the environment was only captured by the eyes when needed. Interestingly, when the processing demands of the 'just-in-time' strategy increased, participants tend to rely more on working memory load (Ballard et al., 1995). Furthermore, Ballard et al. (1995) and Hardiess et al. (2008) showed, regarding the investment of gaze movement (for the purpose of information acquisition from the external world) in competition with that of memorization (for the purpose of internal information representation within working memory), a trade-off between the acquisition and memorization strategies that was driven by the current costs of the given sub-tasks to process. An increase in costs for the acquisition strategy has been obtained through enlarging the exploration distance between stimuli, thereby leading to larger gaze movement amplitudes (Ballard et al., 1995; Hardiess et al., 2008). Conversely, increasing demands on working memory, through for example increased memory load, resulted in greater reliance on gaze processing (Droll & Hayhoe, 2007; for the opposite effect see Aivar et al., 2005). These studies support the idea that a decision making process exists, striving to minimize processing demands in general (Gray et al., 2006; Hardiess et al., 2008) though trading-off between the two strategies depending on their efficiency to retrieve information from the environment or from memory.

In order to strengthen the knowledge about decision makers which trade-off between fixations and working memory, and to extent this research by the understanding of individual strategies, I introduced a comparative visual search experiment (as in Hardiess et al., 2008) appropriate to manipulate acquisition as well as memorization costs in a complete within-subject designed experiment (**publication #4**). Furthermore, eye movements and memorization could now easily and indirectly quantified by analyzing just the switching of a visual mask covering one stimulus array at a time (i.e., number of gaze shifts was measured as number of mask switches; average fixation duration was measured as average time between the mask switches). While the overall trade-off adaptations in the whole population of participants could be reproduced, I found that each subject was using its own, specific trade-off strategy which differed substantially between subjects. By defining a strategy space spanned by number of gaze shifts (number of mask switches) and processing time (time between mask switches), it was found that the distribution of the individual strategies followed a power law ranging from strong preference for acquisition (relying on gaze shifts) to an equally pronounced preference for memorization (relying on working memory). Interestedly, condition dependent adaptations of strategy that followed the same overall trade-off pattern were also found, albeit at a somewhat smaller scale. To conclude, population-based trade-off-curves were discussed as a result of two factors, inter-subject variation of preferred strategies, and within-subject adjustment of resource allocation (**publication #4**).

Another study was enrolled in order to extent the findings about acquisition-memorization trade-offs when testing locomotion instead of oculomotor behavior (**publication #1**). When using locomotion as acquisition strategy, another motor system is involved, which demands higher time and/or energy resources. In order to make the results comparable with that found for gaze adaptions, I redesigned the block-copying paradigm of Ballard et al. (1995) for the use in the new locomotion experiment. In short, patterns of colored blocks were presented at a 'model area', together with additional blocks provided in a 'resource area'. Subjects had to walk freely to pick up blocks from the resource and drag them to the 'workspace area' to build a copy of the model. With such a design, the costs for acquisition (distance between the areas) as well as those for memorization (complexity of the block pattern) were manipulated. Overall trade-off adaptations were found similar to the oculomotor version of Ballard et al. (1995). However, instead of relying predominantly on motor strategies to solve the task, now I found a general shift of the trade-off range (i.e., the range in the strategy space, where condition related trade-off adaptations occurred) towards overall higher memory involvement (**publication #1**). Such a shift was most likely induced by the overall higher costs for acquisition when walking. The trade-off idea states that behavioral strategies are selected so as to minimize certain task and condition dependent costs. To answer the question about the nature of such costs, I focused on temporal considerations, since others found substantial relevance for that (Gray et al., 2006; Hardiess et al., 2008). Through analyzing relevant timing parameters (initial model visit duration, overall walking time, and overall response time), I found that behavioral data could be modeled following the idea that the trade-offs were generated by the minimization of combined temporal costs (soft constraints; **publication #1**).

In summary, using a within-subject design in comparative visual search, where each subject was tested in conditions containing varying costs for acquisition as well as memorization, it was shown that the population behaved as known from previous studies, i.e., population-based trade-off-adaptations were found. Here, if acquisition costs rose, subjects shifted their strategies towards cognitive resources. Consequently, if memorization costs were increased, trade-offs were found to rely more on motor behavior. Additionally, inter-subject variations of the preferred strategies were found and discussed with respect to individual weightings of the respective costs. Furthermore, trade-off adaptations were identified as stable and robust (i.e., no learning about the arising costs was involved) and independent of the motor system (gaze shifts vs. locomotion). Finally, the nature of costs could be explained modeling the temporal characteristics of the strategies used.

4.4 Part 4: Spatial behavior - Wayfinding involving spatial memory and language

relevant articles: publication #2, publication #10

Navigation is characterized as the coordinated and goal-directed movement through an environment. Montello (2005) proposed two components of navigation;

locomotion and wayfinding. Locomotion combines all modes of the agent's movements around an environment which are directly accessible to the body's sensorimotor system. Processes involved in locomotion cover surface identification combined with the selection of adequate posture and gait, obstacle identification and avoidance, and landmark navigation (i.e., beaconing, the movement towards a perceptible landmark). In contrast, wayfinding is the more cognitive and planning component of navigation serving the selection of efficient routes through the environment to reach a certain goal. Consequently, wayfinding requires spatial memory (declarative long-term memory and working memory) in order to represent and process knowledge about places and their connections to represent routes and maps.

In their classic work, Siegel & White (1975) proposed that spatial knowledge develops with landmark and route knowledge as the precursors of map-like survey knowledge; a scheme that has been labelled the dominant framework (Montello, 1998), and discussed in terms of granularity of spatial representations (**publication #2**). Route knowledge is typically based on an egocentric reference frame (i.e., an observer-based, viewpoint-dependent, and ground-level perspective) and learning a route is simply forming associations between locations (places) and the actions to take in the sequence of the route (place-action associations). On the other hand, survey knowledge is associated with an allocentric reference frame (i.e., a world-based and viewpoint-independent perspective), because it includes configural knowledge about the relations (topologic, action-based, metric, or graph-like) between locations in the environment (cf. also Chrastil (2013) for a more fine-graded taxonomy). In summary, it seems that navigators can draw upon different memory representations but the open question is, what determines the use of one form over the other. In addition, the dichotomy between routes and survey knowledge, is well established in neurophysiological findings showing that the basal ganglia are involved in stereotyped route following while map-like navigation activated cortical areas and the hippocampus (Burgess, 2008; Hartley et al., 2003; Wolbers & Büchel, 2005).

4.4.1 Interplay between working and long-term memory in spatial thinking

The nature of visuo-spatial working memory and its interaction with long-term memory is a current focus in the study of spatial cognition and the cognitive neuroscience of wayfinding. The concept of a 'spatial image' was introduced by Loomis et al. (2013) suggesting that environmental information is constantly updated and represented in an ego-centric working memory of the surrounding space (Land, 2014). Information from distant locations beyond the current sensory horizon can originate from two sources, i.e., long-term memory of distant places and episodes or spatial updating if the distant place had been visited before and was since maintained in working memory. In recent times, thinking about spatial coding favor rather a multiple representation of space to handle the problem of scale (i.e., near- and far-distance action space; vista space vs. environmental space; Grusser, 1982; Montello, 1993). Indeed, imaging studies have identified an extensive network of cortical and subcortical brain areas involved in a variety of spatial behaviors, where the interplay of spatial long-term and working memories have been shown to recruit structures such as the retrosplenial cortex as well as medial temporal lobe (e.g., Ranganath & Ritchey, 2012).

Concerning the interplay between the working and long-term memory, a new model, comprising view-based representations (Schölkopf & Mallot, 1995) combined with supporting behavioral data, was presented (**publication #10**). The model predicts that within a given area or place, subjects memories for some views (related to a certain target square) may be more salient than others, that the imagery of a certain target square should depend on the location where such a recall takes place, and that recall favors views of the target square that would be obtained when approaching it from the current recall location. In the associated behavioral study considering spatial thinking, pedestrians from Tübingen were encouraged to imagine the view of familiar urban places (i.e., two city squares) while approaching at various interview locations (**publication #10**). At each of eight to ten interview locations, the pedestrians were asked to draw a sketch map of the respective city square. Orientations of such sketch map productions were analyzed and found as significantly depended on distance and direction of the interview location from the respective target square, i.e., different views were recalled at different locations. Deeper analysis revealed that location-dependent recall was related to the respective approach direction when imagining a walk from the interview location to the target square. These results were consistent with the view-based model of spatial long-term and working memories and their interplay in spatial thinking.

In conclusion, the study addressed the issue how ego- and allocentric representations of space interact in human working and long-term memories and present a view-based model considering the interplay between these two memories. The key finding was that imagery of familiar city squares depends on the current position of the person imagining the square. And further, a detailed analysis of imagined orientations allowed to disentangle working- and long-term memory components. Finally, a coherently view-based account of the organization of spatial representations that simplifies models of spatial learning from visual input could be presented.

4.4.2 Verbal place codes promote survey knowledge in wayfinding

The connection between language or language-supported representations and the coding of space has been studied on a wide variety of aspects including the acquisition of spatial knowledge from verbal descriptions (e.g., Avraamides et. al, 2004; Mellet et al., 2002), verbal direction giving (e.g., Fontaine & Denis, 1999), influences of spatial reference frames which are employed in specific languages on the judgment of similarity of spatial configurations (e.g., Majid et al., 2004), or retrospective reports of spatial thinking (e.g., Tenbrink & Wiener, 2009). However, concerning wayfinding behavior, only few support regarding the combined or supporting representation of verbal and non-verbal material exists (Meilinger et al., 2008; Miller et al., 2013). Certainly, spatial cognition and even wayfinding are complex behaviors, involving a variety of highly cognitive processes including working memory (to process path integration and spatial updating), long-term memory (involved in survey navigation), and spatial reasoning (needed for route planning, or directed search for conjectured place adjacencies). Interactions between verbal and non-verbal representations could be assumed to be developed differently for different such abilities and thus, also for various levels of granularity. Granularity, or the level of spatial hierarchy, is a conception where the different functions that lead to a complete representations of space (i.e., the knowledge about space) could be systematized (see **publication #2**). Depending on the task at hand, individual competences, the environmental complexity, and the time available, the coding of space can be supported at different levels of granularity or in combination thereof.

In a wayfinding paradigm, I was testing the idea that symbolic labeling (visually by using icons or verbally by using words) increases the learning and representation of relevant spatial material (places) albeit differently in route and survey knowledge tasks (**publication #2**). In a virtual reality environment, participants had to learn either a single route (containing ten connected places) in a route condition or four partly overlapping routes forming together an eight-shaped map in a survey condition. To support the representation of places while learning the routes, participants had to associate either meaningful and descriptive icons (symbols), names or nothing (control condition) to each of the places. In a following test phase, the participants' performance (in measurements of walking distance and time) was quantified for each condition and in each task. Here, participants' had just to navigate the ten places without any error in the route task while they had to infer and navigate four novel routes in the survey task. Interestingly, we found varying influences of place labeling regarding the different tasks. In the rather simple route task, where just stimulus-response associations had to represented to provide adequate route knowledge, neither icons nor names were found as helpful in the test phase. In contrast, both place labeling options were found as beneficial (i.e., decreasing the walking distance, participants needed for the novel routes) when survey knowledge was established and applied (**publication #2**). Moreover, participants rated as good navigators demonstrated a much higher advantage when using place labeling in comparison to the other group of poor navigators.

In conclusion, labeling was found to support the formation of abstract place concepts which are useful in the more complex (higher hierarchy and representational level) survey, but not in the rather simple and egocentric route tasks where only stereotyped stimulus-response associations are needed. With this study, the advantage of language-supported representations in wayfinding was (to our knowledge) shown for the first time in such a direct way.

5 Summary

Adapted and hence complex behavior could be generated when perceptual, cognitive, and motor processes interact. Furthermore, situations with competing demands on such processes are commonplace in routine human activities. Consequently, mental operations have to be postulated capable to solve such complex demands and to produce adequate and 'optimal' behavioral reactions by allocating the available resources to ongoing task demands in a manner that achieves goals efficiently.

One of the general aims of my research in the last couple of years was to study and further understand, how the ability to adapt to changing conditions is expressed when sensory, motor, cognitive processes or a combination thereof are changed or affected due to task manipulations or as a consequence of brain lesions. Regarding sensory or memory deficits, homonymous hemianopic patients were investigated in a series of detection, search, and collision avoidance experiments, all capable to characterize the functional and adaptive gaze movement behavior in comparison to healthy subjects. Here, basically two subgroups of patients could be identified differing in the ability and extend to compensate for their visual field loss. Such differences were discussed within the scope of working memory functions supporting (or not) the compensation of hemianopics. These findings were novel and will be helpful and necessary regarding a more 'realistic' evaluation procedure done in the eye hospitals.

The collision avoidance paradigm used in the studies with hemianopic patients was further developed to investigate the potential role of working memory for the task of obstacle detection and representation when multiple and dynamic objects have to be observed. Here, a representation in working memory was found that is shaped by the collision relevance of each single moving object. Furthermore, the gaze pattern applied to form such representation was found as determined by pre-knowledge concerning street crossing behavior.

In another line of research, I was interested in the flexibility and efficiency of perceptual-motor vs. processing-memorization behaviors in tasks where the costs of the needed sub-strategies are already known by the decision makers. In comparative search and block copying tasks, I could show that an acquisition vs. memorization trade-off exists capable to allocate the needed resources (sub-strategies) in order to 'optimize' the overall temporal costs. Furthermore, subjects were found with individual and characteristic strategy choices depending on the personalized limited resources of working memory and executive function.

Finally, the interplay between working and long-term memory as well as that between spatial memory and language was investigated in wayfinding tasks. Here, both real, field experiments as well as virtual reality tasks were utilized to study spatial behavior. As a result, a novel (view-graph) model of the combined but weighted influence of working and long-term representations could be presented. This model was further supported and validated by experiments about spatial thinking. Further, the supporting function of symbolic descriptions in a pure 'monologic' situation was revealed and found as more pronounced when complex survey knowledge was needed.

With the studies and results, I have obtained so far, new directions and perspectives about adaptive behavior and memory in the compensation of visual field deficits, in the adequate sampling of significant interceptive objects, in the efficient allocation of behavioral strategies, and finally, in the production of spatial representations with the help of language and views were presented. These findings yield the potential to enrich the knowledge and understanding about the character and function of adaptivity in complex and natural tasks.

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2. Hardiess G., Halfmann M., Hamm F. & Mallot H.A. (submitted). Explicit place naming supports spatial learning in survey, but not in route navigation. *Psychological Science*.
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PLoS one

Acquisition vs. Memorization Trade-Offs Are Modulated by Walking Distance and Pattern Complexity in a Large-Scale Copying Paradigm

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Abstract

In a ''block-copying paradigm'', subjects were required to copy a configuration of colored blocks from a model area to a distant work area, using additional blocks provided at an equally distant resource area. Experimental conditions varied between the inter-area separation (walking distance) and the complexity of the block patterns to be copied. Two major behavioral strategies were identified: in the memory-intensive strategy, subjects memorize large parts of the pattern and rebuild them without intermediate visits at the model area. In the acquisition-intensive strategy, subjects memorize one block at a time and return to the model after having placed this block. Results show that the frequency of the memory-intensive strategy is increased for larger inter-area separations (larger walking distances) and for simpler block patterns. This strategy-shift can be interpreted as the result of an optimization process or trade-off, minimizing combined, condition-dependent costs of the two strategies. Combined costs correlate with overall response time. We present evidence that for the memory-intensive strategy, costs correlate with model visit duration, while for the acquisition-intensive strategy, costs correlate with inter-area transition (i.e., walking) times.

Citation: Hardiess G, Basten K, Mallot HA (2011) Acquisition vs. Memorization Trade-Offs Are Modulated by Walking Distance and Pattern Complexity in a Large-Scale Copying Paradigm. PLoS ONE 6(4): e18494. doi:10.1371/journal.pone.0018494

Editor: Xiaoxi Zhuang, University of Chicago, United States of America

Received October 15, 2010; **Accepted** March 9, 2011; **Published** April 8, 2011

Funding: This research was partially supported by the Deutsche Forschungsgemeinschaft within the Werner Reichardt Center for Integrative Neuroscience (CIN). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Getting around in a constantly changing world relies on contributions from multiple behavioral or cognitive processes competing for common resources such as metabolic energy, information processing capacity, or processing time. The allocation of such resources to the individual processes requires some sort of ''decision making'' or ''executive function'' [1–4], taking into account the relative value of each choice's expected consequences, i.e. its costs and pay-offs. In this paper, we study this resource allocation process for the interaction of (or trade-off between) memorization of large amounts of information and the repeated acquisition of smaller amounts of information when acquisition involves walking between various locations. Similar interactions are common both in animal behavior and in human activities such as optimal foraging or economic decision making.

For memorization and processing of visual information, the visual working memory (WM) is an essential resource. WM can be defined as a system for maintaining and processing a certain amount of information temporarily [5,6]. In a large body of research two general limitations of WM have been demonstrated: a temporal limitation [e.g., 7–10] and a storage capacity limitation [e.g., 11–13]. With respect to time, WM representations decay within several seconds when no active rehearsal processes [14] take place. Regarding storage capacity, visual WM can maintain information on approximately three to five items at a time. Additionally, these items appear to be coded in the form of integrated object representations, rather than as a collection of disconnected visual features [e.g., 12,15,16]. Visual representations in WM are maintained and updated throughout the course of a task either by using continuous, 'just-in-time' acquisition of environmental information, as has been shown for saccadic gaze behavior [17], or by making inferences on already existing memorized information, or both.

'Just-in-time' acquisition of visual information by repeated looking as opposed to keeping more information in memory [17] is a central example of strategy trade-offs minimizing certain overall costs. Such costs arise at various levels and processes including physiological costs for storing information [18], for gaze movements and redirecting attention [19], or for perceptual or attentional processing [20]. In addition, the time needed to complete a task is in itself an important cost factor, since it precludes or inhibits other relevant performances [21]. Since these costs are likely to vary with environmental and task constraints, cognitive routines are needed to balance the investment into each resource [22].

Trade-offs between gaze movements and WM use have been studied in a number of tasks which involve looking back and forth between two or more experimental areas [17,23–25]. In the block-copying paradigm of Ballard et al. [17], a pattern of colored blocks is presented at a ''model area'', together with additional blocks provided in a ''resource area''. Subjects pick up blocks from the resource area with the computer mouse and drag them to the ''workspace area'' where they built a copy of the model. The more the working memory is used, the fewer fixations on the model area are required. In the comparative visual search paradigm of Hardiess et al. [24] and Pomplun et al. [25], differences between two patterns have to be detected by looking back and forth between these patterns. In both paradigms (block copying and comparative visual search), the putative costs of data acquisition are manipulated by varying the distances between the different areas and thus requiring larger or smaller gaze-shifts. In the block sorting paradigm of Droll and Hayhoe [23], blocks with different properties have to be picked up from a reservoir site and moved to one of two "conveyor belts", depending on their property. In this paradigm, costs of memory load are manipulated by varying the predictability of the necessary information. Independent of where cost changes were applied (i.e., gaze or memory systems), all studies show an adaptation of the trade-off between gaze movement behavior and memorization processes. When the costs for gaze behavior were increased experimentally, participants shifted the balance point towards a more intense use of WM. In contrast, in the case of low stimulus predictability, participants reduced the involvement of WM and maximized the amount of gaze shifts, achieving 'just-in-time' processing. In summary, all investigations identified a trade-off function capable of optimizing the arising costs throughout the course of a task. Droll and Hayhoe [23] conclude that such trade-offs are an intrinsic, unconscious, pervasive, and stable aspect of human behavior.

In the above studies of the acquisition vs. memory trade-offs, acquisition behavior amounted to gaze shifts carried out by movements of the eyes and/or the head. Clearly, this kind of motor behavior is executed within small spatial scales and within very short periods of time. For example, a saccade is usually performed in less than 100 ms [26]. Together with the fixation time for extracting information (e.g., 0.4 s for fixations during making tea: [27]; 0.3 s for fixations during comparative visual search: [24]; or 0.2 s for reading: [28]) the time required for a gaze movement and thus for visual acquisition of one piece of information amounts to about one second. If acquisition is realized by gaze movements, the load that can be experimentally imposed on this side of the trade-off is therefore rather limited. It is not clear, how the strategies of resource allocation extend to acquisitive behaviors consuming much more time - in the range of several seconds.

In the present study we approach this question by replacing the gaze-shift component of the block-copying task [17,29,30] by actual bodily locomotion (i.e. walking) in a large room. Locomotion consumes much more time and energy than gaze movements and should therefore increase the costs for acquiring or updating information substantially. Model, resource, and workspace areas were placed at the corners of an equilateral triangle. Participants had to walk between these three operating areas to acquire new pattern information throughout the course of the copying task. In contrast to previous studies, two different types of cost were manipulated in a full factorial design: First, the costs for walking between the operating areas were varied by using two arrangements with different walking distances ("near" and "far" conditions). Second, different memorization costs were generated by using two types of block patterns, "simple" and "complex", differing in their memory load.

The goal of the present study was to assess and quantify strategy trade-offs in a walking paradigm including manipulations in acquisition and memorization costs. With overall higher costs for locomotion compared to saccadic motor behavior, we expect a general shift of the task solving strategies towards a greater reliance on memory. Furthermore, we hypothesize that both types of cost manipulations are capable of modulating walking strategies. This modulation can be modeled as a linear optimization of combined costs.

Methods

Participants

48 naïve subjects volunteered to participate in this study (24 male and 24 female). Participants were under- and postgraduate students from the University of Tübingen and their ages ranged from 19 to 36 years (mean 24.6 years). Participants were paid for their participation and gave informed written consent. This research was performed in accordance with the 1964 Declaration of Helsinki and was approved by the ethical committee of the University Hospital of Tübingen.

Material

Block patterns. Each block pattern was composed of six quadratic LEGO® duplo® blocks of six different colors, forming a connected pattern. Blocks were placed on a grid where every block covered two by two grid cells. To control memorization demands, we varied the neighborhood rules between adjacent blocks. In "simple patterns", adjacent blocks shared a complete edge (Figure 1a); in "complex patterns", block adjacency could also be defined by sharing a half edge (like in a staggered brick wall) or just one corner point (diagonal neighbors, see Figure 1b). Thus, for blocks of the simple type, just one possibility or rule exists to contact another one (full edge connection), whereas for blocks of the complex patterns three of such possibilities were available (full edge, half edge, or diagonal configuration). Each complex pattern comprises one to two full edge, two to three half edge, and one to two diagonal connections. In summary, the two pattern types varied with respect to their information content (degrees of freedom), and with respect to possible chunking into salient a sub-pattern. For each type, ten different patterns were created.

Experimental setup. Three separate areas arranged in the shape of an equilateral triangle were defined for model (M), resource (R), and workspace (W) operations (cf. Figure 2a). Subjects had to copy each particular block pattern presented at the model area into the workspace area by using blocks provided at the resource area. Each of the three areas consisted of a box without top cover (height 0.3 m, depth 0.22 m, width 0.3 m) placed on a 0.9 m high pedestal allowing convenient handling of the blocks. The model patterns were presented within the box at the model area. Within the box at the resource area, participants were provided with four blocks of each color for picking up. The box at the workspace was initially empty, but on the bottom a grid texture was provided allowing a more accurate alignment of blocks. The boxes were used to prevent subjects from looking at the blocks or patterns at a particular area when operating elsewhere. To vary the costs for locomotion, two different sizes of the triangular arrangement were used. In the near condition, area-to-area distance was 2.25 m while twice this distance (4.5 m) was used in the far condition (see Figure 2a).

Position tracking

To record the walking trajectories produced by subjects while operating between the three areas (i.e., 2-dimensional body-in-space movements) an infrared light-based tracker system (ART-track/DTrack from A.R.T. GmbH, Weilheim, Germany) with 6 degrees of freedom was used. This device tracked a rigid target object (i.e., configuration of five light reflecting balls) that was fixed on a special helmet participants had to wear. The temporal tracking frequency of the system was 60 Hz. From the trajectories, area visits were detected using a criterion of 0.5 m. For analysis of

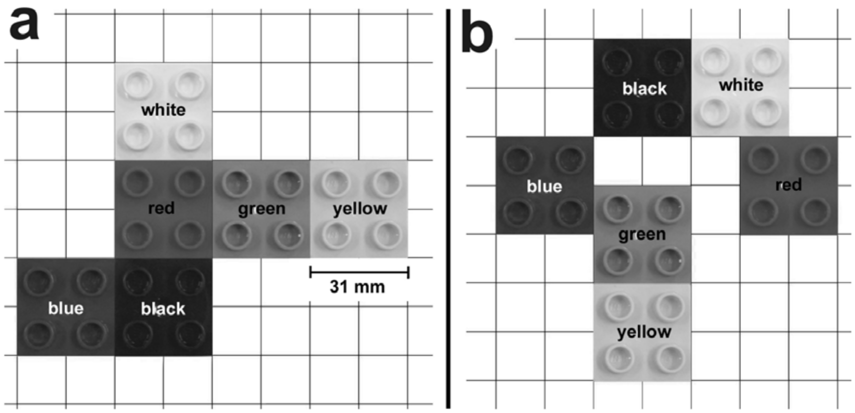

Figure 1. Example block-patterns. Model examples of the simple (a) and the complex (b) condition. Each pattern consisted of six quadratic LEGO® duplo® blocks (length: 32 mm, height: 24 mm) colored differently. Highlighted edges illustrate the different possibilities in which blocks could make contact with each other (black: full edge contact, white: half edge contact, and gray: diagonal block configuration, for a detailed explanation see section 'block patterns').
doi:10.1371/journal.pone.0018494.g001

the areas subsequently visited during a trial, subjects' body-in-space positions were evaluated (cf. Figure 2b).

Procedure

Experimental groups. In a 2×2 factorial, between subject design, the 48 subjects were randomly assigned to one of four different experimental groups (12 to each group; gender was counterbalanced). Across these groups, we varied pattern complexity and locomotion distance in order to quantify the trade-off between memorization and acquisition intensive strategies. Thus, the four experimental groups include the combinations: simple/near, simple/far, complex/near, and complex/far.

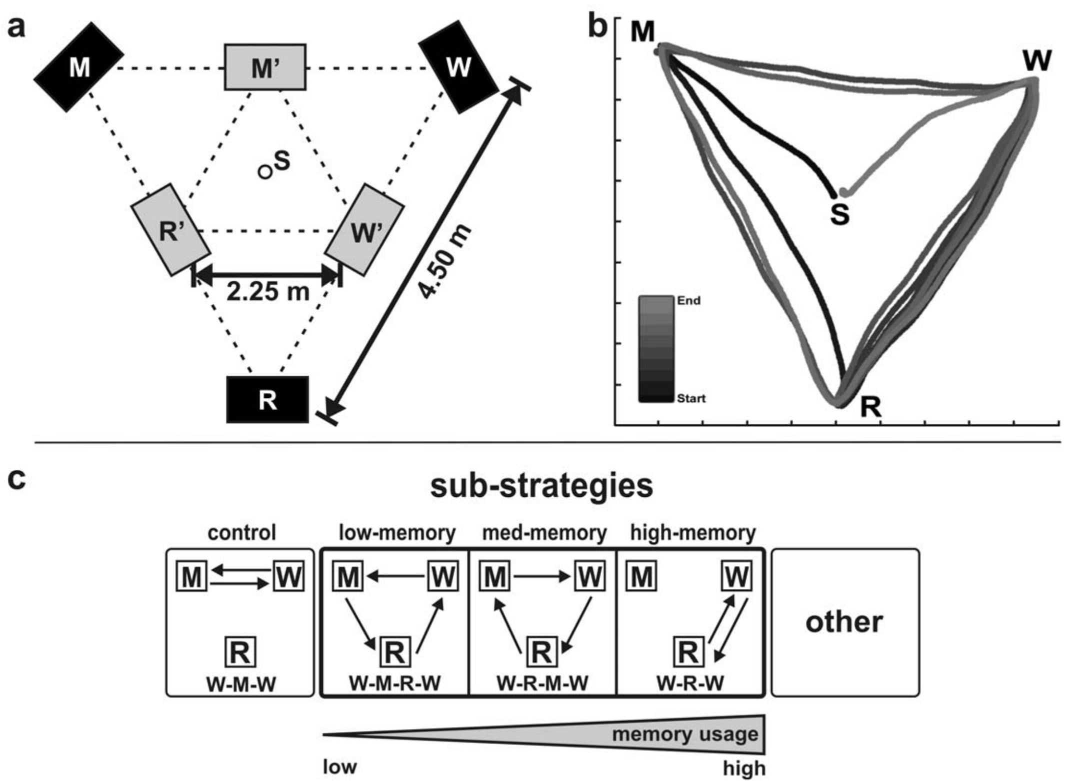

Figure 2. Task setup and analysis of walking trajectory. a) Scheme of the experimental setup with the spatial arrangement of the three operating areas (M: model, W: workspace, R: resource area, S: start and end point of a subjects' trajectory) for the two distance conditions (black boxes: far distance condition, gray boxes: near distance condition). b) Example of a subject's single trial trajectory in the long distance and complex pattern condition. Temporal course is coded with a gray-scale gradient. b) Relevant sub-strategies (together with their names) and their demand on WM from low to high usage. The W-M-W sub-strategy was applied as 'control' strategy without any block operation. 'Other' denotes all remaining sub-strategies which had individual frequencies of occurrence below 2% (for a detailed explanation see section 'walking sub-strategies').
doi:10.1371/journal.pone.0018494.g002

Experimental procedure. Subjects were familiarized with the particular task operations in a pre-test where one four-block pattern had to be copied. Afterwards, each subject had to complete ten experimental trials consecutively, each with a different block pattern. Subjects started and finished each trial by standing still for about ten seconds at the central point of the triangular configuration (cf. Figure 2a and b). After each trial the copied pattern was photographed by the experimenter for later analysis of copying errors. Subsequently, all three areas were prepared for the next trial, i.e., placing a new block pattern in the model box and putting back all blocks from the workspace to the resource area. Thus, subjects found a new block pattern at the model area, a sufficient amount of blocks at the resource area, and an empty workspace area.

Subjects could visit each of the three areas in any sequence as often as necessary for replicating the current block pattern. They were instructed to do so as quickly and reliably as possible. No feedback was given to subjects during the experiment, neither about their copying performance nor about the walking strategies.

In all conditions subjects had to follow three rules throughout the copying task: i) it was forbidden to carry more than one block while walking between the areas ii) once a block was placed at the workspace area no repositioning was allowed, and iii) after placing the last block at the workspace area subjects had to go back immediately to the central point of the area configuration denoting the end of the trial.

Data analysis

Copying errors. We analyzed the errors made during copying the block patterns for each of the four experimental groups. Errors were analyzed as pattern errors and block errors. Pattern errors denote the proportion of incorrectly copied patterns. Block errors denote the amount of single blocks copied at a false position or with the false color and were calculated as the proportion of the total number of blocks in the 10 patterns ($n = 6$ blocks $\times 10$ patterns $= 60$) averaged over subjects. A pattern was considered erroneous if at least one block error occurred.

Walking sub-strategies. The focus of the present study was to identify and characterize the trade-off between WM load and re-acquisition via locomotion. For that purpose a method was needed that assessed the extent of memory usage quantitatively. Following Ballard et al. [17] we divided the locomotion sequence of each trial into different walking sub-strategies (see Figure 2c). All sub-strategies could be classified without ambiguity.

A sub-strategy is a section of the walking sequence between two subsequent visits of the workspace area; it usually (except for the 'control' sub-strategy W-M-W) corresponds to the placement of one block. As an example, the sequence of visited areas …-W-R-W-M-R-W-R-M-W-… was divided into the sub-strategies W-R-W, W-M-R-W, and W-R-M-W. The W-R-W (i.e., 'high-memory') sub-strategy is the strategy with the highest memory involvement. Here, all required information concerning (at least) the next block (i.e., color and position) is retrieved from memory and no additional visit of the model is needed. In contrast, the sequence W-M-R-M-W (i.e., 'just-in-time') denotes the sub-strategy with the lowest memory involvement, where subjects walk to the model area to look for the color of the next block. After picking a suitable block from the resource area, they come back to the model area once again, presumably because they did not remember the position of that block. Thus, color is remembered during the M-R step and position during the M-W step of the sequence. In contrast to the 'high-memory' sub-strategy, the associated walking distance is doubled when using the 'just-in-time' strategy. The 'low-memory' sub-strategy (W-M-R-W) uses an intermediate amount of memory and path length; color has to be remembered during the M-R step, while position has to be remembered during both the M-R and R-W steps. An overview of the different sub-strategies (together with the name that is used throughout the manuscript) and the demands on memory is provided in Table 1 and Figure 2c.

Starting at the central point, the initial sub-strategy of all subjects for all trials was M-R-W. Since this sequence was a simple consequence of the task design, it was not significant for later analysis of walking strategies and thus excluded. In addition to the analysis of walking trajectories, the time subjects needed for walking and the time spent at each area was recorded. The duration for an area visit was measured from entering until leaving a catchment area defined by a radius of 0.5 meters around each operating area. The time subjects spent at the model area was separated into time for the first and subsequent visits in the course of the analysis of memorization processes.

Results

Task performance: Errors and overall response times

Task performance was quantified by the number of pattern errors and block errors. In all conditions participants showed a high level of performance, i.e., on average 9 out of 10 patterns were copied correctly (Figure 3a). Furthermore, only about two to three blocks out of all 60 blocks were copied at a false position. Statistical analysis showed no influence of distance condition or pattern complexity on pattern errors (Kruskal-Wallis-Test: $\chi^2 = 1.4$, $p = .71$) nor on block errors (Kruskal-Wallis-Test: $\chi^2 = 3.78$, $p = .29$).

Response time was analyzed in terms of the overall time participants needed to finish a single trial (Figure 3b). For an analysis of durations of model visits, see section 'memorization and model usage' below. Regarding overall time, a two-factorial ANOVA with pattern complexity (complex vs. simple) and distance condition (far vs. near) as factors was conducted. We found significant main effects of pattern complexity ($F(1,44) = 34.59$, $MSE = 173.54$, $p < .001$, $\eta_p^2 = .44$) and the distance condition ($F(1,44) = 56.81$, $MSE = 173.54$, $p < .001$, $\eta_p^2 = .56$). We found no interaction between these two factors ($F(1,44) = 1.17$, $MSE = 173.54$, $p = .28$). Independent of pattern complexity, subjects needed significantly more time to reproduce the patterns in the far as compared to the near distance condition (Figure 3b). Additionally, compared to the simple pattern condition, trial duration for the complex patterns was significantly increased in both distance conditions.

Locomotion strategies

As described in the methods section (cf. 'walking sub-strategies'), trajectories of each trial were analyzed by means of a number of sub-strategies indicating various amounts of memory usage. Separately for each experimental group the frequency of occurrence of these sub-strategies was evaluated. A summary of sub-strategies together with their demand on WM is given in Figure 2c and Table 1. Overall, two predominantly used sub-strategies (i.e., 'high-memory' and 'low-memory') and several sub-strategies with generally low occurrence (below 5%) were found in all four experimental groups.

The sub-strategies with low frequencies of occurrence (see Figure 4) were 'control' (means between .96 and 3.15%), 'med-memory' (means between .5 and 3.38%), and 'other' (means between .92 and 4.93%). The category of 'other' contains the sum of all remaining walking strategies with individual frequencies of occurrence below 2% on average. Interestingly, the sub-strategy with the lowest memory involvement at all, i.e., 'just-in-time', was

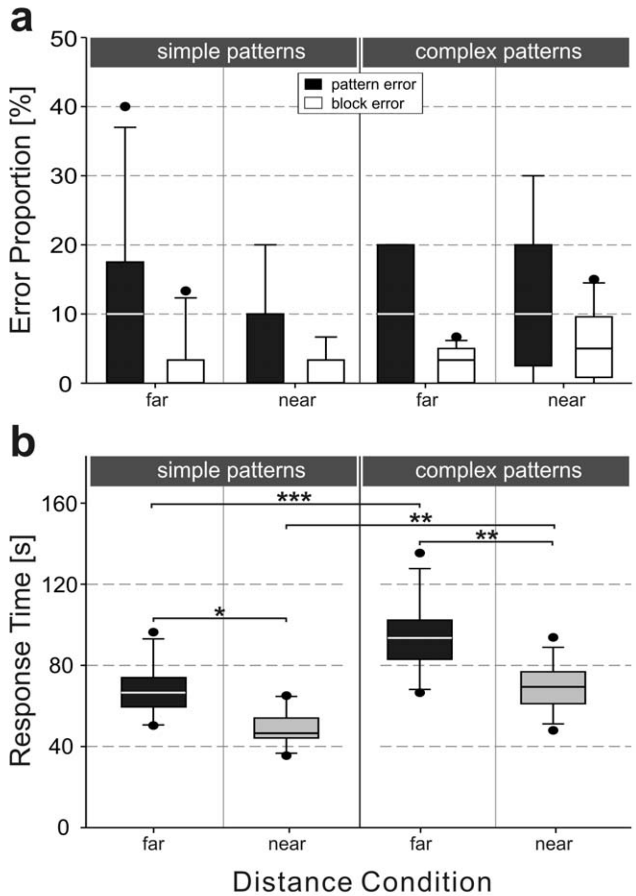

Figure 3. Task performance: error rate and overall response time. a) Box-Whisker plot of proportion of errors made during copying the ten simple patterns (left) and the ten complex patterns (right) for the far and the near distance conditions. Black boxes display the pattern errors: the proportion of false on all patterns (n = 10) averaged over subjects of the respective group. White boxes display the block errors: the proportion of false blocks on all blocks in all ten patterns (n = 6 blocks×10 patterns = 60) averaged over subjects of the respective group. b) Box-Whisker plot of response time to complete a single trial averaged over all subjects of the respective group for the simple (left) and complex (right) pattern situations and for the far (black boxes) and near (gray boxes) distance conditions. Statistical effects (post-hoc analyses) are presented for each pattern complexity/distance combination (*p<.05; **p<.01; *** p<.001).
doi:10.1371/journal.pone.0018494.g003

part of the 'other' category; it was applied only in the complex/near and the complex/far group with means of 1.45% and .16%, respectively. We never found this sub-strategy in any of the near distance trials. The 'control' sub-strategy was applied as the control strategy without any block operation.

The two main (i.e., predominantly used) sub-strategies were 'high-memory' (WRW) and 'low-memory' (WMRW, see Figure 4). The 'high-memory' sub-strategy was applied if subjects could rely on memories of both color and position of (at least) the next block. No model visit was required with this sub-strategy. In contrast, if neither color nor positional information of the next block was available from memory the 'low-memory' sub-strategy was applied. In this case, subjects had to visit the model for memorizing both block features before picking up and placing the block.

Statistical analysis reveals an influence of both, distance and pattern complexity on the frequency of occurrence of the two main sub-strategies. By calculating a two-factorial ANOVA for the proportion of 'high-memory', we identified main effects of pattern complexity (simple vs. complex: $F(1,44) = 22.15$, $MSE = 187.42$, $p < .001$, $\eta_p^2 = .33$) and distance (far vs. near: $F(1,44) = 4.9$, $MSE = 187.42$, $p < .05$, $\eta_p^2 = .1$). Thus, with an increase in distance and a decrease of pattern complexity the trade-off between acquisition and memory is shifted towards the memory-intensive sub-strategy 'high-memory'. This shift of the trade-off is also reflected in the other main sub-strategy 'low-memory'. Here, the influence of both factors was inverted (complexity: $F(1,44) = 15.38$, $MSE = 160.16$, $p < .001$, $\eta_p^2 = .26$; distance: $F(1,44) = 7.33$, $MSE = 160.16$, $p < .01$, $\eta_p^2 = .14$). A decrease in distance and an increase in pattern complexity induced a shift of the trade-off between acquisition and memory towards the 'low-memory' sub-strategy. For both main sub-strategies no significant interaction between the two factors (distance and complexity) was found ('high-memory': $F(1,44) = .75$, $MSE = 187.42$, $p = .39$; 'low-memory': $F(1,44) = .44$, $MSE = 160.16$, $p = .51$). However, based on the estimated parameters of the linear model of the ANOVA on the proportion of 'high-memory' (goodness of fit $= R_{adj}^2 = .35$) a difference in distance condition depending on model complexity was apparent, indicating an ordinal interaction.

Memorization and model usage

In order to assess the degree to which the model is used in the various conditions, we analysed the duration and number of model visits and the number of blocks processed after the initial model visit of each trial.

The total time for all visits subjects spent at the model (Figure 5a) depended on pattern complexity but not on distance (two-factorial

Table 1. Sub-strategy characterization.

	sub-strategies			
memorization parameter	**W-M-R-M-W just-in-time**	**W-M-R-W low-memory**	**W-R-M-W med-memory**	**W-R-W high-memory**
# and type of block features memorized before sub-strategy	0	0	1 (color)	2 (color+position)
# and type of block features memorized during sub-strategy	1+1 (color, position)	2 (color+position)	1 (position)	0
# of visits at the model during sub-strategy	2	1	1	0

Characterization of all sub-strategies used by subjects for the purpose of copying a block regarding the involvement of memory (M: model, W: workspace, and R: resource area). Each sub-strategy is given a name which is used throughout the manuscript.
doi:10.1371/journal.pone.0018494.t001

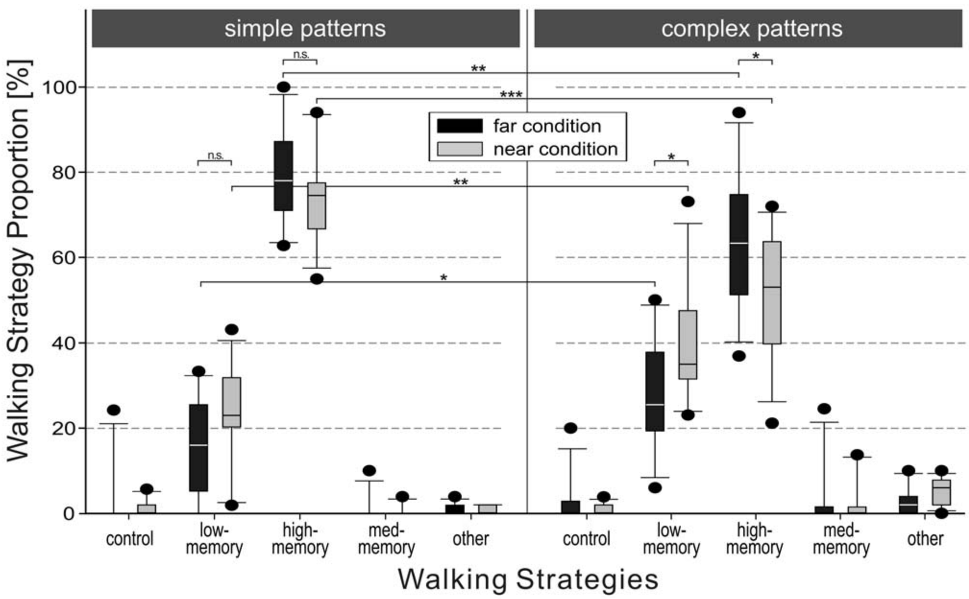

Figure 4. Proportion of walking sub-strategies. Box-Whisker plot of proportion of walking sub-strategies used by subjects during copying the simple patterns (left) and the complex patterns (right) averaged over all subjects of the respective group. Black boxes display the frequencies of walking sub-strategies for the far distance condition and gray boxes these for the near distance condition. Post-hoc analyses are calculated for 'low-memory' and 'high-memory' referring the proportion of walking sub-strategies between far and near and simple and complex pattern conditions (*$p<.05$; **$p<.01$; *** $p<.001$; n.s. not significant). The characteristics of all individual sub-strategies are explained in detail in the results chapter (see section 'walking sub-strategies').
doi:10.1371/journal.pone.0018494.g004

ANOVA, complexity: $F(1,44) = 20.1$, $MSE = 39.92$, $p<.001$, $\eta_p^2 = .31$; distance: $F(1,44) = .9$, $MSE = 39.92$, $p = .35$). Within each experimental condition, subjects spent significantly more time for the first model visit compared to subsequent model visits (Figure 5a). Similar to the results for the overall response time, the time for initial memorization (i.e., first model visit) was also found to increase with longer distance and higher pattern complexity (Figure 5a). However, for the initial memorization times, dependence on conditions did not reach significance in a two-factorial ANOVA with pattern complexity (complex vs. simple) and distance condition (far vs. near) as factors (complexity: $F(1,44) = 2.8$, $MSE = 37.02$, $p = .1$; distance: $F(1,44) = 3.41$, $MSE = 37.02$, $p = .07$). Since no significant differences were found for subsequent model visits within each experimental group all subsequent time values were averaged for each group. Regarding time for subsequent model visits, a two-factorial ANOVA with pattern complexity and distance condition as factors was conducted. We found only a significant main effect of pattern complexity ($F(1,44) = 12.881$, $MSE = 1.297$, $p<.01$, $\eta_p^2 = .23$). No significant influence of the distance ($F(1,44) = .012$, $MSE = 1.297$, $p = .91$) was found.

To estimate the amount of memory subjects allocated in the different experimental conditions we analyzed the number of model visits per trial and the number of consecutive 'high-memory' cycles after the initial model visit (Figure 5b and c). Initial and consecutive 'high-memory' cycles were chosen for two reasons: i) the initial 'high-memory' cycles include only knowledge obtained through a single memorization process (first model visit) without pre-knowledge of the pattern and ii) consecutive 'high-memory' cycles exclude intermediate memory refresh.

The number of model visits per trial was dependent only by pattern complexity but not by the distance (two-factorial ANOVA, complexity: $F(1,44) = 13.86$, $MSE = .55$, $p<.001$, $\eta_p^2 = .24$; distance: $F(1,44) = 2.14$, $MSE = .55$, $p = .15$). Subjects visited the model for memory refresh more often in the complex conditions (means: 2.77 for the far and 3.19 for near distance) than for simple patterns (means: 2.08 for the far and 2.28 for near distance).

We found an overall higher number of consecutive 'high-memory' cycles in the simple pattern conditions (means: 3.2 for the far and 2.57 for near distance) than in the complex pattern conditions (means: 2.18 for the far and 1.54 for near distance). Within pattern complexity, also an increase of memorization was found with an increase of the distance. The two-factorial ANOVA with pattern complexity (complex vs. simple) and distance condition (far vs. near) as factors showed significant main effects of pattern complexity ($F(1,44) = 14.03$, $MSE = .89$, $p<.001$, $\eta_p^2 = .24$) and distance condition ($F(1,44) = 5.33$, $MSE = .89$, $p<.05$, $\eta_p^2 = .11$). No significant interaction between these two factors was found.

In a trial by trial analysis of blocks processed after the initial model visit, we found moderate correlations between the duration of the initial model visit and the number of consecutive 'high-memory' cycles. Correlations reached significance for all conditions (simple/far: Rho-S = .23, $p<0.05$; simple/near: Rho-S = .51, $p<0.01$; complex/far: Rho-S = .6, $p<0.01$; complex/near: Rho-S = .34, $p<0.01$).

Trade-off stability

The influence of trial order on the occurrence of used sub-strategies was analyzed by comparing the frequencies of sub-strategies per trial within each experimental group. No influence of the trial order on any of the walking sub-strategies could be found. Figure 6 illustrates this stability of sub-strategy usage within each experimental group for the main sub-strategy 'high-memory'.

Discussion

Working memory (WM) supports many higher cognitive functions by maintaining representations of a limited number of

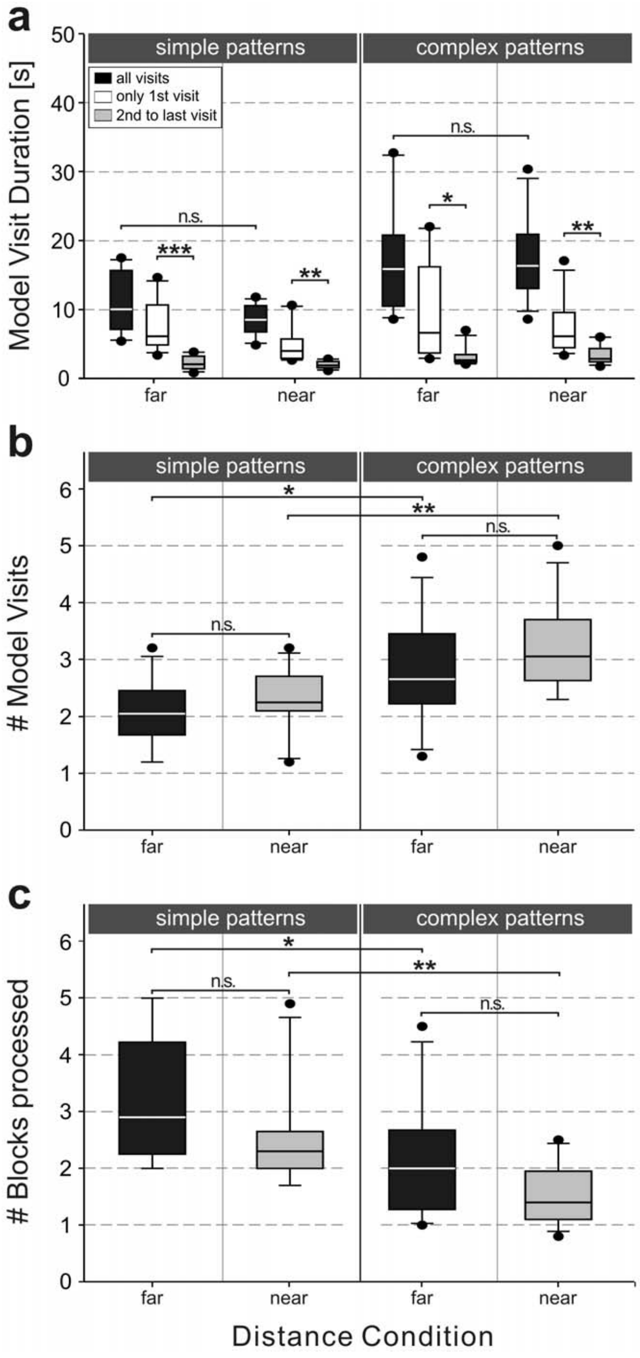

Figure 5. Model operations. a) Box-Whisker plot of time subjects spent to visit the model area averaged over all subjects of the respective group for the simple (left) and complex (right) pattern situations and for the far and near distance conditions. Black boxes display the total time, subjects spent at the model. White boxes display the duration of the first model visit. Gray boxes display the average duration of individual subsequent model visits. Statistical effects (t-test) are calculated between first model visit and second to last model visit times for each pattern complexity/distance combination. Post-hoc analyses are calculated between the distance conditions for each complexity. b) Box-Whisker plot of the number of model visits per trail averaged over all subjects of the respective group for the simple (left) and complex (right) pattern situations and for the far (black boxes) and near (gray boxes) distance conditions. Statistical effects (post-hoc analyses) are presented for each pattern complexity/distance combination. c) Box-Whisker plot of the number of blocks processed after the initial model visit per trail (i.e., number of consecutive 'high-memory' cycles after the initial model visit) averaged over all subjects of the respective group for the simple (left) and complex (right) pattern situations and for the far (black boxes) and near (gray boxes) distance conditions. Statistical effects (post-hoc analyses) are presented for each pattern complexity/distance combination. ($^{\star}p<.05$; $^{\star\star}p<.01$; $^{\star\star\star}p<.001$; n.s. not significant).
doi:10.1371/journal.pone.0018494.g005

items, and by selecting and attending to those representations which are most relevant for the current task. Memory items include multiple types of information, such as verbal or visuospatial, as well as task rules and are represented in WM through sustained patterns of neural activity [31]. Executive decisions or choices are needed between all possible and competing courses of actions based on the relative value of their expected consequences [2–5]. The allocation of resources to the competing strategies or actions requires trade-off decisions which will show in the preference for one or another strategy or action, and in the dependence of such trade-offs on task constraints. [22,32].

The main objective of the present study was to investigate if such a trade-off, already described for the balancing of WM and gaze movements [17,23–25], also exists for locomotion behavior, i.e., actions that demand larger time frames (seconds) and distance scales (meters). If such a trade-off exists, variation of memory load and required walking distance should affect the behavioral strategies employed by the subjects. To prove this hypothesis, the block-copying task introduced by Ballard et al. [17] was adapted to fit the needs of our walking paradigm. Additionally, pattern complexity was added as a second dependent variable to investigate the relative weights of locomotion and memory load.

Strategy trade-off

The main result of this paper is that alternative behavioral strategies, which can be used to achieve the same goal, are used to various extents if task parameters are varied. In our block-copying task, the main behavioral strategies are i) initial acquisition of large amounts of information and subsequent operation from memory ("memory-intensive strategy"), and ii) the repeated acquisition or re-acquisition of smaller pieces of data and subsequent processing of these individual packages ("acquisition-intensive strategy"). The

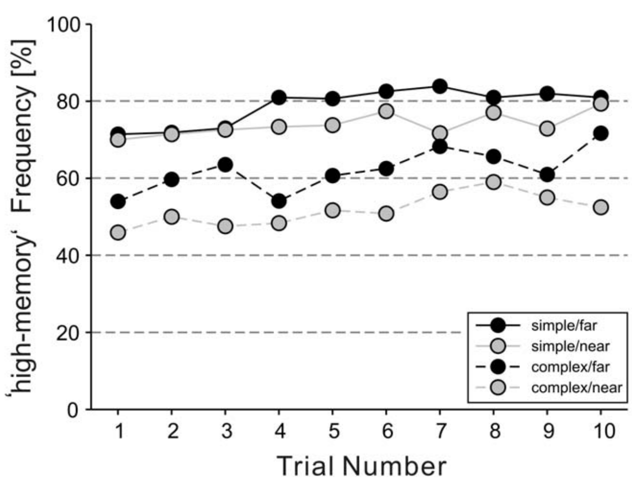

Figure 6. Sub-strategy stability over trials. Occurrence of the main sub-strategy 'high-memory' as a function of trial number. The frequency of the sub-strategy was averaged over all subjects within the respective group and is plotted separately for each experimental group.
doi:10.1371/journal.pone.0018494.g006

memory-intensive strategy is realized by long initial model visits and high proportions of the 'high-memory' sub-strategy. The acquisition-intensive strategy, in contrast, uses relatively short initial model visits and a high proportion of the 'low-memory' sub-strategy.

For more complex patterns, the use of the memory-intensive strategy is reduced, while more re-acquisition steps are performed. A similar but weaker effect was found for walking distance: if walking of larger distances is required, the frequency of the memory-intensive strategy increases.

The observed pattern of the dependence of sub-strategy usage (Figure 4) on conditions is evidence for a functional trade-off balancing the relative costs of WM involvement (memory-intensive strategy) and locomotion behavior (acquisition-intensive strategy). The nature of these costs will be discussed in more detail below. Here we note that the variations in the costs of each strategy induced by varying pattern complexity seem to be larger than the variation induced by walking distance. Thus, the condition-dependent strategy shift for simple vs. complex pattern is more pronounced than for the near vs. far conditions.

As compared to the findings of Ballard et al. [17], who used gaze shifts rather than locomotion, we find a much smaller frequency of the 'just-in-time' sub-strategy W-M-R-M-W. This sub-strategy was the main strategy with a frequency of about 35% in the gaze-study, whereas our results show a predominant use of the 'high-memory' sub-strategy in all experimental conditions (between 50% and 80%) and only a negligible proportion of the 'just-in-time' processing strategy (less than 2%). We conclude that for our task parameters (walking distance and pattern complexity), the trade-off operated on an overall higher memory level, whereas in the case of the gaze movement experiment, the trade-off seems to operate on a lower memory level. This general shift towards higher memory involvement was most likely induced by the overall higher costs for acquisition; pattern complexity had a stronger influence on the selection of sub-strategies at this high memory level.

Processing time and memory operations

As measures of memory involvement in a given strategy we analyzed the duration and number of model visits (i.e. the time spent with the encoding of information) and the number of blocks processed (i.e., the information taken from memory while copying), see Figure 5. As a consistent result, we found that for the simple pattern condition (both in the near and far case), model visit duration is shorter, the number of model visits is smaller, and the number of blocks processed after a model visit is larger than in the complex pattern condition. This indicates that the complex pattern condition (as compared to the simple one) requires more and longer model visits to build up memory. The memorized information, however, suffices only for the placement of a smaller number of blocks. Also, when comparing near and far conditions, the number of blocks processed after a model visit is larger in the far condition, indicating that more memory has been stored.

These findings support the idea that longer and more frequent model visits lead to the build-up of extended memory which in turn is available for the processing of blocks. This idea can be tested directly by calculating within each condition trial-by-trial correlations between the duration of the first model visit and the number of blocks processed consecutively. Here we did indeed find moderate but significant correlations.

The first model visit was significantly longer than the second or any later visit, indicating that it plays a special role. Conceivably, the subject could use this first visit to built up a memory of some global features of the pattern which is not necessarily used for immediate block positioning but may be useful for later information intake. Examples of such features are chunks or templates known to reduce working memory load [33,34].

Simple and complex patterns require different amounts of storage capacity. A simple estimate of this capacity can be derived from the following consideration: Suppose the first block of a simple pattern is placed. For the next block, there are four possible positions observing the neighborhood rules described in the methods section (Figure 1). Ignoring effects of boundaries and mutual intersection of individual block positions, the number of possible six-block patterns will be about $4^5 = 2^{10}$, corresponding to an information content of 10 bits per pattern. A similar calculation for the complex pattern, where 16 positions of the second block are possible, yields $16^5 = 2^{20}$ possible patterns corresponding to an information content of 20 bits per pattern. If we assume that the same total memory capacity is used for both cases, we should expect that the number of blocks processed per model visit in the simple conditions is about twice the number processed in the complex conditions. As can be seen from Figure 5c, this ratio is about 1.5 to 1 in our data. Clearly, the above calculation suffers from a number of shortcomings which may cause the observed deviation. First, the actual number of patterns is smaller than assumed, since the possible positions for block placement are constraint by previously placed blocks. Second, if the assumed trade-off actually takes place, the memory capacity allocated to the task should be larger in the complex condition, predicting ratios below 2 to 1. Third, memory capacity needed for the storage of a pattern will depend on chunking or the possibility of recognizing templates in the pattern. Simple block configurations are more likely to comprise familiar sub-patterns such as letter shapes (e.g., 'I' or 'L') or other geometric figures that facilitate memorization. Chunking processes serve to bind isolated pieces of information together to form a meaningful combination (block positions and sub-patterns) that can be associated with previously stored long-term memories. However, we found that subjects processed between 1.54 and 3.2 blocks in a row (i.e., without model visits in between), a rate that is below the range of the generally assumed WM capacity of 3 to 7 items [e.g., 12,16,35]. Thus, it seems that one block in our task is represented by more than one of the WM items as discussed in the gaze-shift literature cited above. Such an increased amount of WM demand could be caused by the elongated maintenance of memory [e.g., 36] required in our large-scale walking paradigm but not in gaze-shift paradigms. Moreover, temporal forgetting of memorized material is caused by memory decay [37] and processes of interference [38].

Costs and optimization

The trade-off idea states that behavioral strategies are selected so as to minimize certain task and condition dependent costs. Generally two types of costs are considered: i) processing time and ii) energy consumption or other, non-temporal measures of cognitive effort. The soft constraints hypothesis Gray et al. [21] suggests that on the memory side "the only factors that matter are the time required to encode, the time required to retrieve an item from memory, and the probability that an encoded item can be retrieved (i.e., is not forgotten) when needed". That is, the soft constraints hypothesis presupposes a control system selecting sequences of routines (sub-strategies) that tend to minimize performance costs measured in time for processing (i.e., temporal cost-benefit trade-offs). At the same time, the amount of memory used may gradually change, in relation to the costs incurred by acquisition-intensive strategies. Alternatively, it has been suggested that behavioral decisions are always made so as to minimize WM allocation [23,39,40] even when the costs of information access (as measured by time) for 'just-in-time' (perceptual-motor) strategies are greater than the costs for memory strategies [41]. Since WM capacity is limited, the control system is biased to assign work to the perceptual-motor system [42]. For block-copying, Ballard et al. [41] reported that participants preferred a 'just-in-time' (i.e., low WM allocation) strategy that took 3 s to execute over the more memory-intensive strategy that took 1.5 s to execute. Hence time was not the factor determining WM processes in that task. We suggest that the reason why the 'just-in-time' strategy is not used in our experiment is the higher cost of inter area transitions associated with physical walking as compared to mere gaze-shifts. In any case, the data reported here seem to support a soft constraint scheme in which memory costs can be ''traded'' for acquisition costs. For further experimental evidence supporting the soft constraints and minimum memory hypotheses, see [24] and [23].

As revealed by the overall response times (Figure 3b), harder tasks (i.e., the far and complex conditions) require longer overall time. It therefore seems likely that time does play a role as a cost factor in our experiment. To further analyze this hypothesis, we evaluated three timing parameters, i) the initial model visit duration, ii) overall walking time, and iii) overall response time. Within each condition, we analyzed the frequency of the various sub-strategies per trial. Note that these data do not appear in Figure 4 which shows only the frequencies averaged over all trials and subjects within each condition. Next we analyzed the dependence of the three timing parameters on the sub-strategy frequencies per trial. Strategy shift as depicted in Figure 4 is mostly between the sub-strategies 'high-memory' (W-R-W) and 'low-memory' (W-M-R-W). We therefore expressed the strategy shift by the ratio of sub-strategy usage, (#W-R-W/(#W-R-W+#W-M-R-

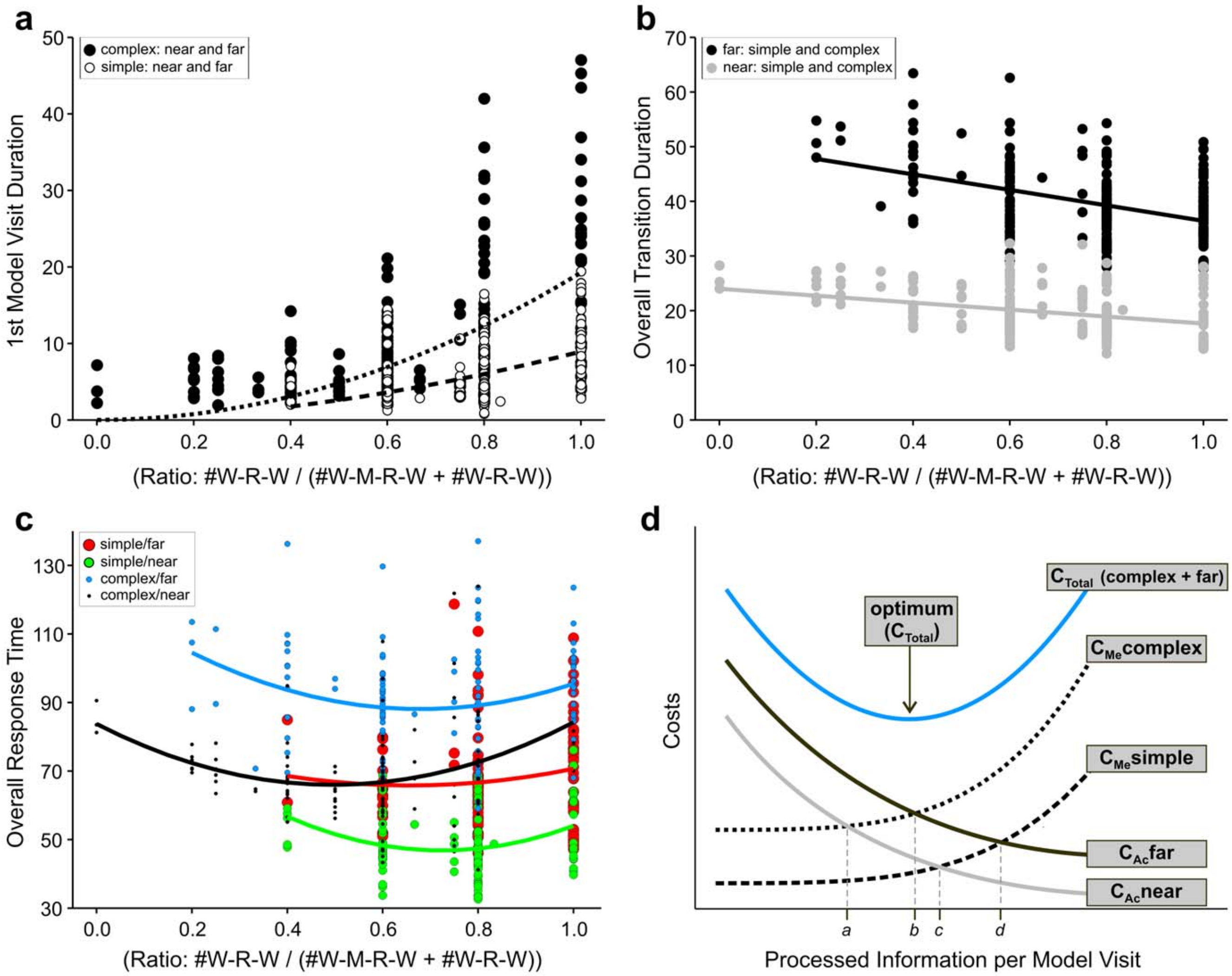

Figure 7. Linear cost optimization. Experimental data for a) costs for memorization (i.e., duration of 1st model visit) with power function fits for simple (dashed line) and complex (dotted line) patterns, b) costs for acquisition (i.e., overall time for transitions) with linear regression lines for near (gray) and far conditions (black), and c) total time costs (i.e., overall response time; regressions indicate quadratic functions). All data are shown as a function of the ratio between 'high-memory' and 'low-memory' sub-strategies. d) Model: Total costs are divided in costs for memorization (C_{Me}) and acquisition (C_{Ac}). If more information is processed at each model visit (i.e., if the task is solved with fewer visits), memory costs increase while acquisition costs decrease. These individual costs vary also with the experimental conditions for walking distance (near and far) and pattern complexity (simple and complex). Total costs for the complex/far condition are depicted as the sum of the according individual cost curves (blue line), leading to an optimum of processed information per model visit at point *b*. The location of each optimum for the four experimental groups is indicated with *a*–*d*.
doi:10.1371/journal.pone.0018494.g007

W)) for each trial. Figure 7a–c shows the timing parameters as a function of this sub-strategy ratio. The duration of the initial model visit (Figure 7a) increases with the proportion of the 'high-memory' sub-strategy. It may thus be considered a cost factor associated with memorization, favoring the 'low-memory' sub-strategy. The curves show power functions fitted to all trials in the simple and complex conditions (lumping together near and far). Conversely, overall walking time (Figure 7b) increases with the proportion of the 'low-memory' sub-strategy. It may thus be considered a cost factor associated with acquisition, favoring the 'high-memory' sub-strategy. The curves show linear regression lines fitted to all trials in the near and far conditions (lumping together simple and complex). The overall response time (Figure 7c) shows a U-shaped dependence on sub-strategy ratio. The curves are second order polynomials fitted to all trials of each of the four conditions. The minima of the U-curves for the four conditions appear in the order complex/near$<$complex/far$<$ simple/near$\approx$complex/near, which is consistent with the actual strategy usage shown in Figure 4.

Figure 7d shows the overall idea of trade-offs generated by the minimization of combined costs (soft constraints). The individual components, i.e. acquisition costs and memorization costs follow convex functions, either decreasing or increasing, whose vertical position depends on the experimental condition. Acquisition costs are assumed to depend only on walking distance and memorization costs are assumed to depend only on pattern complexity. The blue curve shows the sum of the acquisition costs in the far conditions and the memorization costs in the complex conditions. Its minimum corresponds to the sub-strategy ratio optimizing overall response time in the complex/far condition. Models for the other U-curves are obtained by summing the respective individual cost curves, but are not shown in the figure. Their minima occur roughly at the intersections of the individual cost curves and are marked by letters *a–d* in the figure. The model is in good general agreement with the data shown in Figure 7a–c.

In this analysis, the individual cost functions are assumed to be stable and known by the trade-off controller. This is in line with the trade-off stability reported in Figure 6: subjects use the same sub-strategies throughout the course of the experiment without need to adjust to the experienced costs.

In summary, the analysis presented in Figure 7 supports the idea that time is a correlate of overall costs and the trade-off results from the optimization of combined soft constraints (continuous cost functions in Figure 7a and b) for which again temporal correlates can be given. We cannot exclude the possibility that non-temporal costs (e.g., energy consumption, distraction of WM from other important tasks, memory decay) play a role, since they are likely correlated with temporal parameters.

Acknowledgments

We are grateful to Heidi Liou for helpful comments and the realization of data acquisition and analysis. We would like to thank the anonymous reviewer for helpful comments on an earlier version of this article.

Author Contributions

Conceived and designed the experiments: GH KB. Performed the experiments: GH. Analyzed the data: GH KB. Wrote the paper: GH KB HAM.

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Title

Flexible spatial representation is supported by explicit place labeling in survey, but not in route learning

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Abstract

The role of symbolic, language-based support in the representation of space was assessed in two wayfinding experiments with labeling of places using a route and a survey (map-like) knowledge task, respectively. Utilization of verbal place codes was encouraged by offering semantic and meaningful names to select from a list in the name condition. In the icon condition, we tested wayfinding performance when visual icons had to be assigned to places and in a control condition where no labeling was required. We found no differences between name-based and icon-based labeling. Labeling supported wayfinding not in the route but in the survey knowledge task. There, the supporting effect was more pronounced in subjects with good wayfinding scores. We conclude that labeling supports the formation of abstract place concepts which are useful in the more complex (higher hierarchy and representational level) survey, but not in the rather simple and egocentric route tasks where only stereotyped stimulus-response associations are needed.

Keywords

place labeling, symbolic support, route knowledge, survey knowledge, wayfinding, granularity

Introduction

The knowledge about the navigational space develops with landmark and route knowledge as the precursors of survey (map-like) knowledge (Siegel & White, 1975); a scheme that has been labelled the dominant framework (Montello, 1998). Route knowledge is typically based on an egocentric reference frame and learning a route is simply forming place-action associations between locations (places) and the actions to take in the sequence of the route. On the other hand, in survey knowledge, places need to be represented independently of viewing direction and position. Furthermore, survey representations include configural knowledge about the relations (topologic, action-based, or graph-like) between places or regions in the environment (cf. also Chrastil (2013) for a more fine-graded taxonomy). The dichotomy between routes and survey knowledge, is also established by neurophysiological findings. Studies from cognitive neuroscience have shown that the basal ganglia are involved in stereotyped route following while map-like navigation activated cortical areas and the hippocampus (Burgess, 2008; Hartley, Maguire, Spiers, & Burgess, 2003; Wolbers & Büchel, 2005). In wayfinding, it seems that navigators can draw upon different memory representations and formats of spatial knowledge - but the unresolved question is, what determines the use of one form over the other.

Granularity of spatial representations

The hierarchical structure of spatial representations comprises different levels of granularity (scale). At the finest level, the recognition of *landmarks* (i.e., salient and permanent patterns or objects, present in the environment) has to be considered. Grouping spatially related landmarks together leads to the concept of a *place*, the fundamental unit of routes and maps. Building a *route* involves the connection of places with the corresponding spatial behavior. At this intermediate level, several routes can exist in parallel also, with spatial overlap but without interactions to each other (Kuipers, 2000; Mallot & Basten, 2009). Route combination occurs first at the level of *survey* representations. Here, the embedding of places as well as routes in a so called 'cognitive map' as a configural representation of the environment enables the creation of novel routes and shortcuts to find the goal (Tolman, 1948). On top of the hierarchy, the coarsest level of granularity is provided by the formation of *regions* (Wiener & Mallot, 2003), where spatially related parts of the map cluster together.
Depending on task demands (Taylor, Naylor, & Chechile, 1999), individual competences (Wolbers & Hegarty, 2010), complexity of the environment, and the time available for spatial learning (Brunyé & Taylor, 2008), the coding of space can be achieved at each level of granularity.

Language and spatial representation

The interplay between language and the coding of space has been studied on a wide variety of aspects including the acquisition of spatial knowledge from verbal descriptions (Avraamides, Loomis, Klatzky, & Golledge, 2004; Mellet, Bricogne, Crivello, Mazoyer, Denis, & Tzourio-Mazoyer, 2002), verbal direction giving (Fontaine & Denis, 1999), influences of spatial reference frames which are employed in specific languages on the judgment of similarity of spatial configurations (e.g., Majid, 2004), or retrospective reports of spatial thinking (e.g., Tenbrink & Wiener, 2009). However, little is known, about possible functions of language-supported representations in wayfinding behavior. In a dual task study, Meilinger, Knauff, & Bülthoff (2008) showed that for route navigation verbal distractor tasks are more detrimental than distractor tasks involving visual imagery or spatial hearing. Additionally, Miller et al. (2013) recently found in human that hippocampal place cells coding for a certain spatial context were also active during later verbal recall (without presenting the spatial context).

It has been suggested that language-supported representations of space gain their meaning from a process called 'simulation' in which corresponding states in the sensorimotor representations are activated (Barsalou, 1999; 2008). If a verbal direction such as 'turn left after the bridge' is given, this would be translated into a motor plan expressed in the sensorimotor representation and executed from there. Clearly, the sensorimotor representation alone suffices to generate such plans as is apparent from wayfinding performance in animals. In this view, the role of the language-supported representation is therefore limited to communication purposes, while it can be neglected for navigational behavior carried out in the individual (monological) exploration, wayfinding, and planning processes.

Plan of the paper

In this paper, we explore an alternative hypothesis stating that explicit, verbal thinking helps also in basic, non-social wayfinding behavior. Intuitive as this hypothesis may seem, there seems to be no direct experimental evidence in the field of spatial cognition. In visual perception and object recognition, interactions of the hypothesized type have recently been demonstrated (Gentner & Christie, 2008; Dessalegn & Landau, 2008). In the latter study, language is used for binding two parts of a conjunction (e.g., 'red color on left'). Landau & Lacusta (2009) suggest that similar conjunctions (e.g., 'long wall left of short wall') might play a role in place recognition as well.

As pointed out by many authors (review: Mallot & Basten, 2009; Wiener, Büchner, & Hölscher, 2009), spatial cognition, and even wayfinding are not 'monolithic' tasks supported by a joint cognitive faculty. Rather, a variety of abilities can be distinguished including (among others) working memory (path integration, spatial updating), long-term memory (route and survey behavior), and spatial reasoning (perspective taking, route planning, or directed search for conjectured place adjacencies). It is well feasible that interaction between verbal and non-verbal representations of space are not only different for different such abilities but also different for the various levels of granularity (see above).

In this paper, we therefore investigated the effect of symbolic, language-based support (by place labeling) within two different (granularity) levels of spatial representation, i.e., route and survey knowledge. In the route task, subjects simply learned to repeat a route from a given starting point to a goal location while using a stereotyped sequence of stimulus-response (SR) associations leading from one decision point to the next. In the survey task, in contrast, subjects first have to learn a set of intersecting routes and then are asked to infer novel routes by recombining sections of learned routes (Gillner & Mallot, 1998; Hartley et al., 2003; O'Keefe & Nadel, 1978; Wolbers & Büchel, 2005). In both tasks, subjects are requested to label the places either with semantically meaningful names or icons to build up a link between sensorimotor and symbolic representation.

Method

Participants

In this study, 126 participants (students, gender-balanced, 36 for Experiment 1 and 90 for Experiment 2) were recruited at the science campus of the University of Tübingen. They signed an informed consent sheet and were paid 8 Euro per hour. All reported normal or corrected-to-normal vision.

Apparatus and stimuli

Wayfinding experiments were carried out in a desktop virtual environment created with the *MultiGen Creator* software and rendered under *OpenSceneGraph* in a C++ environment. The environments were hexagonal mazes (iterated Y-mazes) with and without loops (Fig. 1a-c). Basic building block was a regular three-way junctions serving either as decision point or dead end (Fig. 1d,e). Each decision point was marked by three cube objects placed regularly in the angles between two streets. Each cube displayed a picture of a salient and nameable landmark object; the same picture appeared on all faces of the cube. The three cubes at one decision point showed different, but semantically related objects or scenes, e.g., musical instruments, trains, beaches, etc. (Fig. 1d). The dead ends were also regular three-way junctions with two of the connected streets ending at a short distance with a barrier (Fig. 1e). They were not marked individually by landmarks. All street segments (except the dead ends) were 100 meters long. Landmarks at adjacent or more distant places could not be recognized due to distance-dependent fading implemented in the computer graphics by the 'dark fog' option (cf. Fig. 1d,e).

--- Figure 1 here ---

Design and procedure

Subjects navigated (first-person, ground-level perspective) the virtual environment by controlling speed and direction with a joystick. They were instructed not to leave the streets and managed to do so after some initial training.

In a within-subject design all three conditions (*baseline*, *icon*, and *name*) were performed by each of the 36 subjects in randomized order for Experiment 1. For the three conditions, different routes were used which were placed in different environments (snow, forest, and dessert), in order to enhance novel learning for each condition (Fig. 2a-c). A session including all three conditions and all three phases (association, route, and test; see below) lasted for about one hour. Completion of all three phases in Experiment 2 involved the acquisition of a survey memory and one condition lasted for about an hour. We did therefore not test individual subjects on all three conditions (*baseline*, *icon*, and *name*), but resorted to a between-subject design in which each subject performed only in one of the conditions. Hence, we needed just one experimental environment (see Fig. 1c). From the 90 subjects participating in Experiment 2, 30 were assigned randomly and gender-balanced to each condition.

--- Figure 2 here ---

Association phase. Both experiments started with an association phase in which predefined routes had to be found (Fig. 2). After reaching a decision place, subjects decided to move left or right. If this decision was in line with the predefined route, the travel was interrupted. In the *name* condition, a list of 10 written place names was presented (Fig. 2c), allowing for meaningful naming of the semantically related set of landmarks characterizing each decision point (e.g., ‘music square’, ‘train station’, ‘beach’, etc.). The subjects picked the appropriate name. At each subsequent visit of this place, the selected name was presented above the particular place (visible from each of the three entering streets). In the *icon* condition, the subjects selected a pictogram related to the semantic content of the landmarks (Fig. 2b). Again, this pictogram was presented above the particular place at later visits. In the *baseline* condition, travel was also interrupted, mainly to indicate that the actual route decision had been correct (Fig. 2a). Here, subjects had to hit the space bar to continue the navigation. In all conditions, subjects continued the wayfinding until reaching a final goal position. If a false decision occurred, travel was not interrupted. Subjects noted their mistake by this lack of interruption or by reaching a dead end. In this case, subjects were required to return to the route on their own, usually by going back one or two places. Previously associated places in the *name* and *icon* condition where labeled with a pictogram (see above) and therefore recognizable as already visited. Therefore, subjects were prevented from going back too far if a false decision occurred. In the *baseline* condition no label was to assign and no such prevention was provided. Here, subjects were more likely to get lost, when returning the route into the direction of the starting point. To correct for this methodical deficit, already visited places in the *baseline* condition of Experiment 1 were also marked (using a blank white sign over the place). In Experiment 2, such a marking was not provided.

The other two phases (in Experiment 1: route and test phase; in Experiment 2: route and survey phase), following the association phase, are described in the respective chapters for the two experiments.

Experiment 1: route knowledge. In this experiment, we investigated whether subjects, encouraged using verbal or icon-based place representations, have an advantage over subjects not specifically biased to do so (three conditions: *baseline*, *icon*, and *name*). In each condition, subjects had to learn and reproduce a certain route including ten decision points (i.e., ten left-right decisions associated with ten places; Fig. 1a).

The experiment proceeded in three phases. In the association phase described above, subjects found out the route, and assigned the corresponding labels to the decision points (in the *icon* and *name* conditions). When going wrong, subjects immediately reached a dead end, indicating their mistake. The goal place (end of the route) was clearly marked by a green disk underlying the whole place. In the route phase, subjects repeatedly travelled the route until they reproduced it without error two times in a row (i.e., optimal path length: 2200 m). As in the association phase, when leaving the route, subjects immediately reached a dead end and therefore have to navigate back to the route for oneself. In the test phase, subjects were released consecutively at five dead ends (Fig. 1a) with the task to complete the route from there. This task requires recognition of the decision places and cannot be performed by simply remembering left-right sequences. Hence, the test phase serves as control for the recognition strategy.

Experiment 2: survey knowledge. In this experiment, we modified the route paradigm for the usage in a survey task. Subjects had to learn eight intersecting routes in the association phase (with the notations given in Fig. 1b). The routes were: BCDEF, BCHGFE, BCHJKA, BAKJHG, and the respective returns. Note that together, these routes covered all ten decision points of the survey environment (Fig. 1b). But, with four or five segments, they were shorter than the routes used in Experiment 1. For individual routes, the association and route phases were identical to those described for Experiment 1 above. For each route, a separate association and route phase was performed after which all place labels (assigned in the respective association phase) were removed. When reaching a place again in the association phase of a later route (this happened because using intersecting routes), subjects had to assign the correct label again. This makes sure that the identity of the places across the various routes had indeed been learned. Subjects who associated different labels at repeated visits of a given place were excluded from analysis.

The route phases were carried out as in Experiment 1. Since the route lengths were shorter than in Experiment 1, this phase was completed faster than before. Different from Experiment 1 was the procedure when leaving the route. Because reaching a dead end could not always serve as an indicator for going wrong (cf. Fig 1b), now, subjects were presented a sign (saying: ‘you are leaving the route’) and replaced back to the start place of the actual route. The route phase was finished, when subjects travelled each route two times in a row without error. In the survey phase, subjects were released in a street heading from a dead end into the adjacent decision place. In addition to that view, an inset was shown for 5 seconds picturing the view of the distant destination place. The task was to find the shortest route to this destination place. Altogether, four novel routes of this type had to be completed successively in the survey phase, from E to A, F to K, G to B, and J to D (Fig 1b). Correct solutions were three or four segments long. None of these routes had been presented during the association and route phases. Subjects were provided with a maximum time of 10 minutes to succeed with each route in the survey phase. After this duration the actual travelling was terminated and the destination place of the next route had to be found.

Data analyses

Dependent variables for both experiments included the total path length travelled (distance), the total response time needed to complete an entire phase (total time), and the number of navigational errors (wrong turns). Errors were defined as decisions not reducing the distance to the goal (the return from a dead end was not counted as an additional error). Since the effects between the measures distance and wrong turns were identical for all phases, we restrict the presentation to showing only the relative excess distance travelled (in percentage above optimal, PAO) and the total time. For example, if a task can be solved optimally by travelling 1000 m and a subject needed 1200 m, PAO would be 20%. Please note, the optimal path lengths in Experiment 1 varied in each phase (association: 1100 m, route: 2200 m, and test: 3000 m). In Experiment 2, routes from the route phase as well as routes from the survey phase contained different amounts of segments. In order to average (within each condition) and compare (across all phases) the performance of the subjects, the variables distance and total time were normalized to one route segment (length: 100 m).

In order to investigate the effects of the three conditions in Experiment 1 together with a possible order effect, a two-way mixed-model ANOVA (within subject factor: condition; between subject factor: order of condition) was calculated for each phase and variable. To investigate a possible effect of the three conditions in Experiment 2, a one-way ANOVA was calculated for each phase and variable.

Results

Experiment 1: route knowledge

Distance travelled. The travelled distance (in PAO) of all three phases and conditions is shown in Fig. 3a for all subjects. A main effect of condition was not found (results of mixed-model ANOVA for association: $F(2, 66) = 1.31$, $p = .28$, $\eta_p^2 = .04$, route: $F(2, 66) = .62$, $p = .54$, $\eta_p^2 = .02$, and test: $F(2, 66) = 2.12$, $p = .13$, $\eta_p^2 = .06$). The main effect of the presenting order of the conditions was only significant for the route phase (results of mixed-model ANOVA for association: $F(2, 33) = 2.23$, $p = .12$, $\eta_p^2 = .12$, route: $F(2, 33) = 6.42$, $p < .01$, $\eta_p^2 = .28$, and test: $F(2, 33) = .11$, $p = .89$, $\eta_p^2 = .01$). Here, the condition that was presented at first during the experiment was always performed worst, without any effect of their own. The condition-order interactions were significant for the route and test phases (results of mixed-model ANOVA for association: $F(4, 66)$

= .15, p = .95, η_p^2 = .01, route: F(4, 66) = 5.08, p < .01, η_p^2 = .24, and test: F(4, 66) = 4.08, p < .01, η_p^2 = .2).

The chance to choose the right direction at each place was 50%. Thus, subjects had to walk about 1.5 times the route plus the way back from the dead ends to the place. Indeed, we found that the travelled distance for all conditions in the association phase was about 60% (PAO). In the route phase, subjects walked about 70% to 90% above the optimal path length. Here, subjects showed the highest variability in performing Experiment 1. Remarkably, about one third of all subjects performed the route phase within the optimal path length showing a high capability to learn and remember all ten places together with the correct directions to walk. The performance in the test phase was similar for all three conditions and with about 30% (PAO) the best of all three phases, indicating a training effect. This high performance cannot be explained by a strategy that simply uses left-right decision chains, rather by a strategy that requires recognition of the decision places.

Given the high variability in the performance of the route phase, the total population was split into two equal-sized sub-groups in order to investigate possible effects related to navigation skills. The splitting criterion was the subject's number of route repetitions in the route phase (16 subjects with the lowest amount of repetitions - good performers; 16 subjects with the highest amount of repetitions - poor performers). The influence of condition on distance travelled for the good and the poor performers is shown in Fig. 3b. A main effect of condition was neither found for the good (results of repeated measures ANOVA for association: F(2, 34) = .32, p = .73, η_p^2 = .02, route: F(2, 34) = .58, p = .57, η_p^2 = .03, and test: F(2, 34) =.35, p = .71, η_p^2 = .02) nor for the poor performers (results of repeated measures ANOVA for association: F(2, 34) = 1.1, p = .34, η_p^2 = .06, route: F(2, 34) = .87, p = .43, η_p^2 = .05, and test: F(2, 34) =2.9, p = .07, η_p^2 = 0.15). However, different tendencies between the two groups regarding the influences of condition in the route phase became obvious. While beneficial in the good performers, both labelling conditions appeared to be detrimental in the poor performing group.

--- Figure 3 here ---

Total time. In addition to the travelled distance, we analyzed the total time and calculated a mixed-model ANOVA to extract significant effects. Fig. 4 shows the results for all three phases and conditions. In the association phase, we found a significant effect of condition (ANOVA; F(2, 66) = 10.46, p < .01, η_p^2 = .24) with an increase in total time for the *icon* and *name* condition. This was due to the fact that selecting an appropriate label (i.e., icon or name) needed more time than just hit the 'space' bar as required in the *baseline* condition. This effect was also found in Experiment 2 (see below and Fig. 6). The time needed in the route and the test phase was similar for all three conditions (results of mixed-model ANOVA for route: F(2, 66) = 1.4, p = .25, η_p^2 = .04 and test: F(2, 66) = 1.4, p = .25, η_p^2 = .04). A main effect of the presenting order of the conditions was only significant for the route phase (results of mixed-model ANOVA for association: F(2, 33) = 2.37, p = .11, η_p^2 = .13, route: F(2, 33) = 3.51, p <

.04, η_p^2 = .18, and test: $F(2, 33) = 2.1$, $p = .14$, η_p^2 = .11). Here, subjects always spent more time in the condition presented at first. The condition-order interactions were significant for all phases (results of mixed-model ANOVA for association: $F(4, 66)$ = 3.0, $p = .04$, η_p^2 = .15, route: $F(4, 66) = 7.42$, $p < .001$, η_p^2 = .31, and test: $F(4, 66)$ = 9.74, $p < .001$, η_p^2 = .37).

--- Figure 4 here ---

Experiment 2: survey knowledge

Distance travelled. In Fig. 5a the travelled distance (in PAO) for all three phases and conditions of the experiment is shown for the whole population of 30 subjects. The columns for the association and route phases contain the averaged results for all eight learning routes and the columns for the survey phase show the average over the four inferring routes.

In the association phase, we found a slight disadvantage of the *baseline* condition, i.e., the travelled distance was significantly increased in this condition (ANOVA; $F(2, 87)$ = 5.54, $p < .01$, η_p^2 = .12). Since correctly visited places in the *baseline* condition of Experiment 2 were not marked (contrary to the other two conditions and Experiment 1), subjects had no cue in case of leaving the route and coming back to a previously visited place and where more likely to travel longer distances.

No effect of condition on travelled distance was found for the route and the survey phase (ANOVA for route: $F(2, 87) = 0.49$, $p = .61$, η_p^2 = .01, survey: $F(2, 87) = 1.03$, p = .36, η_p^2 = .02). However, in the survey phase, an improvement regarding the travelled distance (i.e., a reduction of the PAO) became obvious in the *icon* and *name* condition (see Fig. 5a). Therefore, the whole population of 30 subjects per condition was split into two equal-sized sub-groups, based on their number of route repetitions needed in the route phase (15 subjects with the lowest amount of repetitions - good performers; 15 subjects with the highest amount of repetitions - poor performers). The travelled distance (in PAO) for both sub-groups are shown in Fig. 5b. Now, for the good navigator sub-group, a significant effect of condition in the survey phase was identified (ANOVA: $F(2, 42) = 3.1$, $p < .05$, η_p^2 = .13), indicating an advantage of place labeling (including names and icons) when planning and travelling novel routes. In the splitting analysis, the disadvantage for the *baseline* condition in the association phase remained significant, but only for the sub-group of poor performers (ANOVA: $F(1, 42)$ = 4.68, $p < .05$, η_p^2 = .18).

--- Figure 5 here ---

Total time. In addition to the travelled distance, we analyzed the total time (per segment) for all three phases and conditions as shown in Fig. 6. In the association phase, we found a significant effect of condition (ANOVA; $F(2, 87) = 6.38$, $p < .01$, η_p^2 = .13) with an increase of total time for the *icon* and *name* condition. This was certainly due to the fact that selecting the appropriate label (i.e., icon or name) needed more time than just hit the ‘space’ bar as required in the *baseline* condition. This effect was also found in Experiment 1 (see above and Fig. 4). No condition effect regarding total time was found in the route and the survey phase (ANOVA for route: $F(2, 87) = 1.12$, $p = .33$, $\eta_p^2 = .03$ and survey: $F(2, 87) = 0.05$, $p = .95$, $\eta_p^2 = .001$).

--- Figure 6 here ---

Discussion

In this study, the supporting effect of symbolic, language-based coding on wayfinding performance using explicit place labels was investigated when acquiring spatial knowledge on different levels of granularity (scale) in the spatial hierarchy. Egocentric route learning, represented on a lower hierarchy (Experiment 1), was not effected when using place labels. In contrast, an advantage of symbolic coding using names as well as icons was found in the more complex allocentric survey task (Experiment 2). Here, subjects were found to reduce their travelled distance when inferring novel routes (survey phase) in both labeling conditions compared to the *baseline* condition where no such labels were provided. This effect was significant for the sub-group of the 50% best navigators, but weak for the total group of all subjects and the 50% poorest navigators. We conclude that explicit place labeling, be it by names or icons, support the inference of novel routes from known route segments as an individually skilled competence needed only in allocentric survey navigation.

In spatial behavior, two fundamental aspects were important to distinguish: the kind of environmental information that has to be encoded (spatial knowledge) and the type of representation processes (memory/modality) involved to generate the spatial model. The former refers to the information that is to be acquired by the observer, such as landmark or place information, route or survey knowledge. The latter aspect refers to whether that information is encoded via verbal, visual, spatial working memory, or some combination thereof. By using dual task designs several studies showed the involvement of both, visual-spatial as well as verbal working memories (Baldwin & Reagan, 2009; Garden, Cornoldi, & Logie, 2002; Meilinger et al., 2008). Gras, Gyselinck, Perrussel, Orriols, & Piolino (2012) performed a study focused on the involvement of memory components during the encoding of spatial material. They found that visual-spatial as well as verbal working memories are involved differently depending on the task, whereas localizing landmarks demanded multimodal coding and encoding a route based mainly on visual-spatial processes. Wen, Ishikawa, & Sato (2011, 2013) were examining the involvement of the verbal, visual, and spatial memory components in the acquisition of three types of spatial knowledge (landmarks, routes, and survey) in relation to the subjects' sense of direction (SOD). Subjects with a good SOD encoded landmarks and routes verbally and spatially and were able to integrate the material into a survey representation with the support of all three memory components. In contrast, people with a poor SOD encoded landmarks only verbally and tended to rely just on visual memory when processing route knowledge, failing to acquire survey knowledge. Also Baumann, Skilleter, & Mattingley (2011) found

substantial differences in the use of (object-location) memory representations between good and poor navigators in a landmark-based navigation task. Here subjects were treated with different working memory tasks in the retention interval between encoding and retrieval. While the spatial task interfered with all subjects, the verbal secondary task impaired the navigational performance only of the poor ones.
Our results also document the overall findings about a high variability of navigational performance in route and survey tasks (cf. Wolbers & Hegarty, 2010). Furthermore, the presented data indicate different strategies used by good and poor performers. Good navigators turned out to rely on all three working memory sub-systems to perform well in all spatial hierarchies (levels of granularity), whereby verbal processing seems to be demanded more in survey tasks. In contrast, poor performers selectively employ memory sub-systems and fail or have difficulties when acquiring survey knowledge.

Conclusion

Depending on the nature of the task (purpose and spatiotemporal scaling), spatial memory has the potential to involve egocentric and allocentric representations in parallel as well as their interactions for processes in encoding, retrieval, and planning (Byrne, Becker, & Burgess, 2007; Ekstrom, Arnold, & Iaria, 2014). However, individuals differ in their visuospatial abilities (Blajenkova, Motes, & Kozhevnikov, 2005; Wolbers & Hegarty, 2010) and the type of spatial hierarchy level they adopt (Nori & Giusberti, 2003), leading to high variability found in wayfinding experiments. In our route task subjects operated within a short time scale and both, encoding and retrieval of the spatial information, was egocentric. Hence, subjects could solve this task effortlessly by operating just on the level of egocentric representation (associative) without relying on the additional value of symbolic representation. In the survey task, subjects were engaged much longer with the egocentric encoding of the spatial environment and needed to recode (in an allocentric manner) the material to infer novel routes. Thus, representations on different levels of granularity had to be handled and symbolic coding may support such a flexible representation as an individualized competence.

Methodological issues/considerations

Encouraging (or discouraging) place naming. The idea of the present experiments was to study wayfinding with and without the involvement of language-supported representations. While it seems plausible that language-based knowledge (i.e., the place name) is used in the *name* condition, we cannot rule out the use of such representations in the other conditions. Indeed, generating names for places may be a general strategy used in all conditions. In this case, selecting the name from a list with predefined choices may actually generate a conflict between the name picked from the list and another name already generated before. This mechanism may in part explain the slight disadvantage for the *name* condition in the route experiment.
Dual tasks and overshadowing. Selecting place labels in the *icon* and *name* conditions is a second task to be performed by the subjects and imposes some

additional cognitive load on them. Meilinger et al. (2008) studied such dual tasks in route navigation and found that verbal tasks interfered with navigation performance and did so more strongly than visual imagery or a directional hearing task. Clearly, in this experiment the dual task was not related to the navigation, but remembering the name or icon assigned to a place may draw from the same cognitive resources. If so, the additional load should be the same in the route and survey knowledge experiments reported here. Since we found an advantage of labeling in the survey task, we conclude that the benefit of labeling outweighs other costs in this case.

Author Contributions

GH, FH, and HAM designed the experiments. Testing, data collection, and data analysis were performed by MH and GH. HAM and GH wrote the manuscript. All authors approved the final version of the manuscript for submission.

Acknowledgments

The work described in this paper was carried out at the Institute of Neurology of the University of Tübingen. Additional support was provided by the German Federal Ministry of Education and Research (BMBF) within the Bernstein Center for Computational Neuroscience (Grant No 01GQ1002A). We are grateful to Reinhard Scholz for his help collecting the data.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Figures and Legends

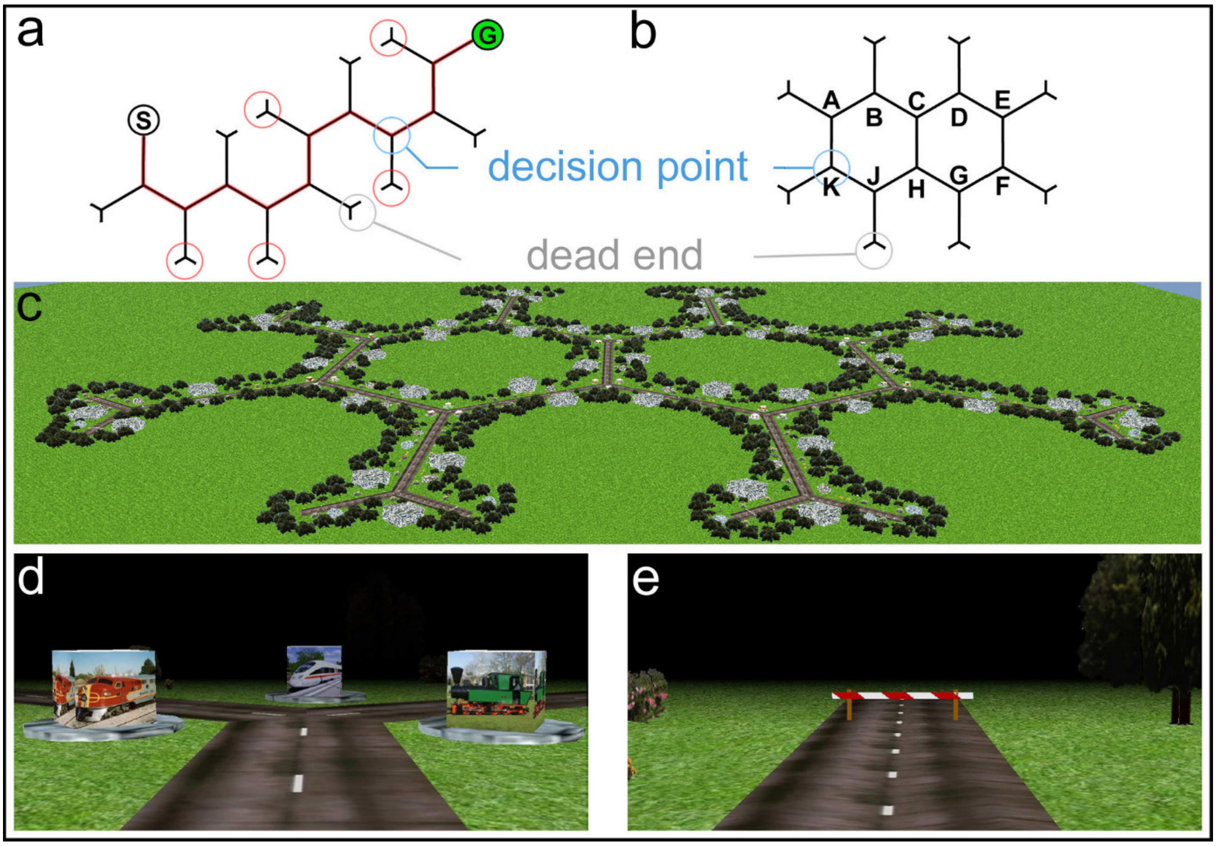

Fig. 1: Virtual environments. a) Layout of the route environment used in the *baseline* condition of Experiment 1 with ten decision points (junctions or places). S: start point, G: goal point. The optimal path to travel is marked in red (total length: 11 segments x 100 m = 1100 m). The five start points for the test phase are marked by red circles. b) Layout of the survey environment used in Experiment 2. Decision points are marked (A–K) for reference in the text. Each segment has a length of 100 m. c) Survey (bird's eye) view of the environment used in Experiment 2. d) View of an exemplary decision point showing three landmark cubes displaying various pictures of trains. The icon to be associated with this place (in the *icon* condition) shows a railway track (see Fig. 2b; icon 8). e) Dead ends are marked by barriers. In d) and e), also note the distance-dependent fading generated by the 'dark fog' option.

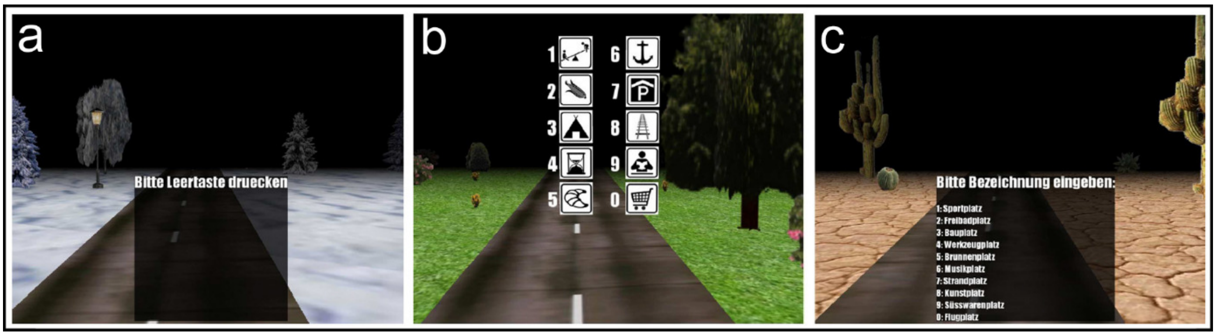

Fig. 2: Place labeling in the association phase (after having passed a place in the correct direction of the route). a) *Baseline* condition. Travel continues after hitting the space bar (text says: 'please hit space bar'). b) *Icon* condition. Travel continues after selecting one icon (out of ten) which will be shown at future visits of the place just passed. c) *Name* condition. Travel continues after selecting one name (out of ten) from a list (text says: 'please choose a name'). The name will be shown at future visits of the place. Note, three different environments (snow, forest, and dessert) were used in Experiment 1 in order to enhance novel learning for each condition. In Experiment 2 just the forest environment was used.

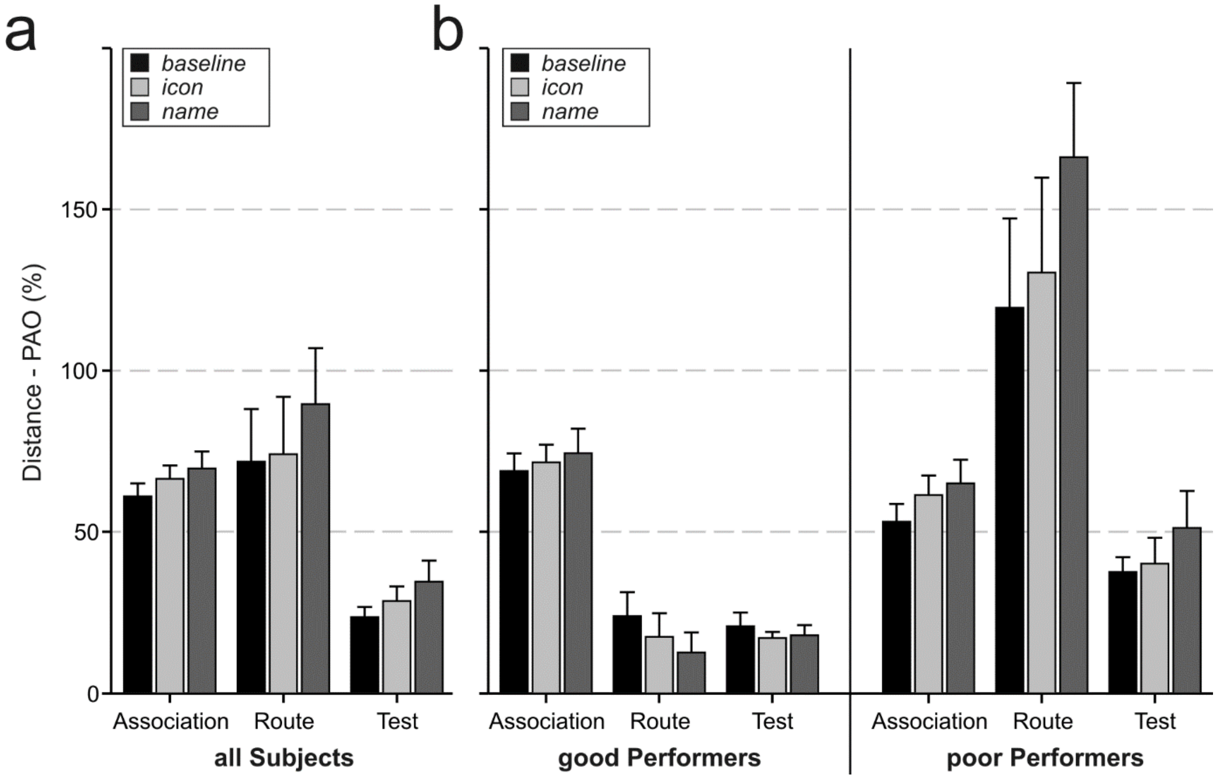

Fig. 3: Experiment 1. Travelled distance in PAO (percentage above optimal) for all three conditions (*baseline*, *icon*, and *name*) in all experimental phases. a) Results averaged over all 36 subjects. b) Results averaged over the 16 good (left) and 16 poor (right) performing subjects. Error bars indicate standard errors of the mean.

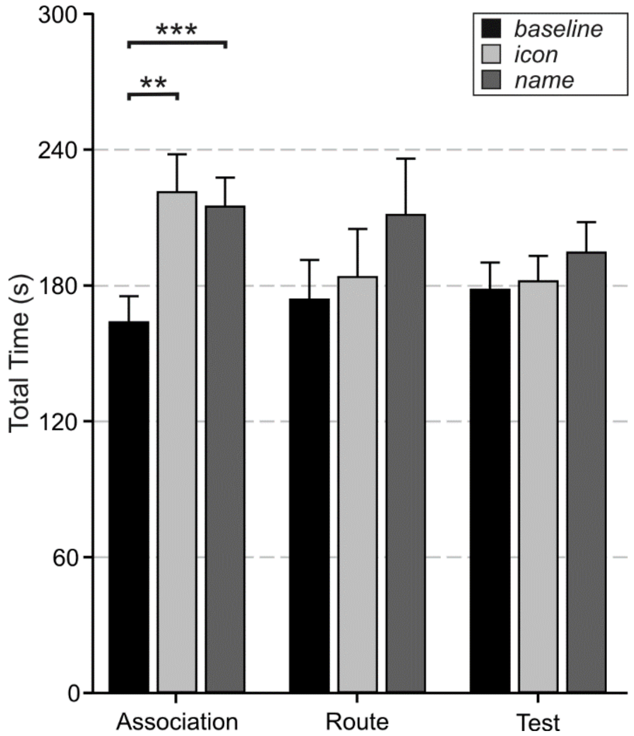

Fig. 4: Experiment 1. Total time (time needed to complete an entire phase) for all three conditions (*baseline*, *icon*, and *name*) in all experimental phases averaged over subjects. Error bars indicate standard errors of the mean. Significances refer to pairwise comparisons based on *t*-tests performed *post-hoc* (ANOVA results are given in the text); ∗∗ : $p < .01$, ∗∗∗ : $p < .001$.

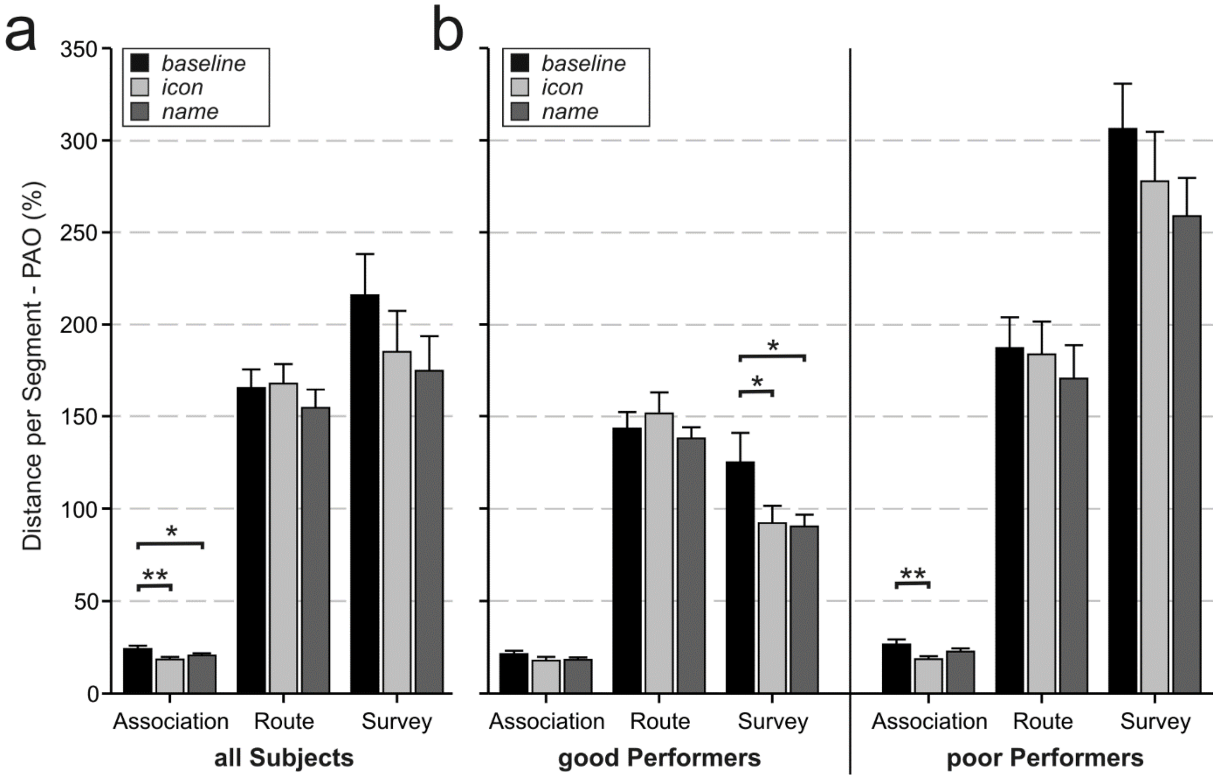

Fig. 5: Experiment 2. Travelled distance normalized to one segment in PAO (percentage above optimal) for all three conditions (*baseline*, *icon*, and *name*) in all experimental phases. a) Results averaged over all 30 subjects. b) Results averaged over the 15 good (left) and 15 poor (right) performing subjects. Error bars indicate standard errors of the mean. Significances refer to pairwise comparisons based on *t*-tests performed *post-hoc* (ANOVA results are given in the text); $*$: $p < .05$, $**$: $p < .01$.

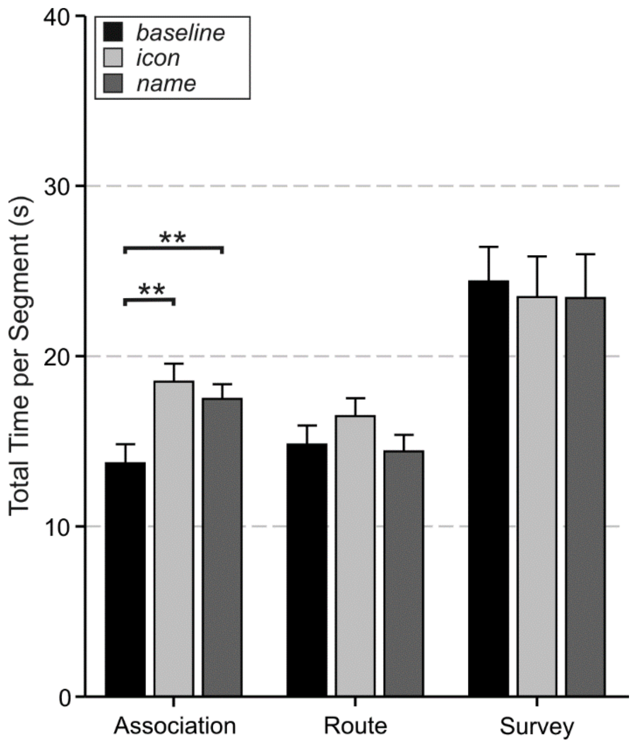

Fig. 6: Experiment 2. Total time (time needed to complete an entire phase) normalized to one segment for all three conditions (*baseline*, *icon*, and *name*) in all experimental phases averaged over all subjects. Error bars indicate standard errors of the mean. Significances refer to pairwise comparisons based on *t*-tests performed *post-hoc* (ANOVA results are given in the text); $**$: $p < .01$.

frontiers in
BEHAVIORAL NEUROSCIENCE

HYPOTHESIS AND THEORY ARTICLE
published: 06 June 2013
doi: 10.3389/fnbeh.2013.00062

Gaze movements and spatial working memory in collision avoidance: a traffic intersection task

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Street crossing under traffic is an everyday activity including collision detection as well as avoidance of objects in the path of motion. Such tasks demand extraction and representation of spatio-temporal information about relevant obstacles in an optimized format. Relevant task information is extracted visually by the use of gaze movements and represented in spatial working memory. In a virtual reality traffic intersection task, subjects are confronted with a two-lane intersection where cars are appearing with different frequencies, corresponding to high and low traffic densities. Under free observation and exploration of the scenery (using unrestricted eye and head movements) the overall task for the subjects was to predict the potential-of-collision (POC) of the cars or to adjust an adequate driving speed in order to cross the intersection without collision (i.e., to find the free space for crossing). In a series of experiments, gaze movement parameters, task performance, and the representation of car positions within working memory at distinct time points were assessed in normal subjects as well as in neurological patients suffering from homonymous hemianopia. In the following, we review the findings of these experiments together with other studies and provide a new perspective of the role of gaze behavior and spatial memory in collision detection and avoidance, focusing on the following questions: (1) which sensory variables can be identified supporting adequate collision detection? (2) How do gaze movements and working memory contribute to collision avoidance when multiple moving objects are present and (3) how do they correlate with task performance? (4) How do patients with homonymous visual field defects (HVFDs) use gaze movements and working memory to compensate for visual field loss? In conclusion, we extend the theory of collision detection and avoidance in the case of multiple moving objects and provide a new perspective on the combined operation of external (bottom-up) and internal (top-down) cues in a traffic intersection task.

Keywords: traffic intersection task, gaze movements, collision avoidance, potential-of-collision, spatial working memory, homonymous hemianopia, visual impairment, field loss compensation

INTRODUCTION

COLLISION AVOIDANCE

Successful and efficient motion in space is based on estimates of the pose and motion of the own body as well as on estimates of (relative) position and independent motion of environmental objects. Motion plans need not only be suited to reach a goal at a given position in space, but at the same time need to take into account both stationary and moving obstacles. Avoidance of moving obstacles requires some sort of anticipation of the obstacles' movement, which may be expected to follow the rules of kinematics as well as traffic regulations if the obstacles are cars on an intersecting street or pedestrians on a sidewalk. The mental representation necessary for path planning and obstacle avoidance in a dynamically changing environment has been described as the *field of save travel* by Gibson and Crooks (1938). This safe field represents all the paths that an agent may take which will avoid collisions with objects in the traffic environment. The field is dynamic, i.e., it changes as the agent or other objects move. Its built-up and maintenance during spatial maneuvers require attentional processes controlling the intake and selection of information and the update of environmental models.

BOTTOM-UP PROCESSING AND MECHANISMS FOR INTERCEPTIVE ACTIONS

When planning a trajectory in a cluttered dynamic environment, the navigator needs to assess the potential of independently moving objects to collide. We will call this variable the potential-of-collision (POC). The main source of information for judgments of POC is the optical (or retinal) flow (see, for example, Lappe et al., 1999; Fajen, 2005) and in particular the perception of time-to-contact (Lee, 1976). The time passed between visual removal and collision or near contact with an object is also known as time-to-collision (Brown and McFaddon, 1986), time-to-arrival (Schiff and Oldak, 1990), or time-to-passage (Kaiser and Mowafy, 1993). Originally, the concept of time-to-contact was introduced into the literature as a hypothesis of how behavior involving interactions with moving objects (such as catching or hitting a ball, i.e., interceptive actions) could be timed (Lee, 1980). An object's time-to-collision can be calculated as the ratio of the object's image size to the rate of change of this size; this ratio was termed *tau* by Lee (1976). The information provided by *tau* is sufficient for the timing of interceptive actions, avoidance maneuvers, and psychophysical judgments of time-to-collision (e.g., Wagner, 1982; Lee et al., 1983; Savelsbergh et al., 1991, 1993). However, despite the fact that *tau* requires just simple computations, only few studies have presented direct neuro-scientific evidence for the usage of *tau* (see Wang and Frost, 1992; Sun and Frost, 1998; Frost, 2010). In fact, empirical results and formal analyses have accumulated which suggest that the *tau*-hypothesis may not be valid and alternative approaches have been put forward (for review see: Wann, 1996; Tresilian, 1999), i.e., *tau* is limited by several factors. For instance, estimates of *tau* are highly sensitive to noise and require an object that is spherically symmetric. Further, *tau* may be used to specify the time-to-contact, but is does not allow to detect changes in velocity. For this task, the first-order temporal derivative of *tau* (i.e., rate of change), *tau-dot*, has been shown to contain the necessary information (Coull et al., 2008). However, evidence for the use of a constant *tau-dot* strategy is conflicting and not convincing (e.g., Bootsma and Craig, 2003 or Yilmaz and Warren, 1995). Furthermore, experiments show that *tau-dot* is just perceived passively from changing visual parameters and estimates based on it have limited predictive power. Festl et al. (2012) studied the related quantity *rho*, i.e., the rate of velocity change, which can also be extracted from retinal measurements alone. Again, experimental results do not support the use of this quantity in self-motion estimation. Recently, Keil and López-Moliner (2012) proposed a new neuro-physiologically plausible implementation based on *tau*, i.e., the corrected and modified *tau*-function. In an initial step, a modified *tau*-function was suggested capable to describe the neuronal responses of object approaches (with constant velocity) found in different species (locust, fruit fly, bullfrog, and pigeon). Furthermore, a corrected *tau*-function was formulated to estimate time-to-collision for "sufficiently small" angular sizes, which, as compared to *tau*, has the advantage of being less sensitive to noise. Finally, the authors showed that the new framework accounted well for the performance of psychophysical experiments where subjects had to estimate time-to-collision of a single, linearly approaching object. However, despite providing a neurophysiologically plausible implementation of *tau*-based functions, the predictive power in the more general context of timing interceptive actions as well as collision avoidance remains to be shown in future studies.

Besides image expansion or looming, the source of information used for *tau* and *tau*-related functions, the angular direction of an object (i.e., object bearing) also contains information for detecting a collision event. Object bearing (i.e., the angle between the heading and an intercepting object) can be measured over a range of time. Objects with high POC will have bearing shifts, which are close to zero (constant bearing angle strategy; Lenoir et al., 1999). In detecting collisions, both sources of information might be involved determining that a particular object is expanding and that the angular direction is constant (e.g., Andersen and Kim, 2001; Ni and Andersen, 2008).

In order to deal with collision detection and avoidance a number of potential variables (where *tau* is just one of them) have been identified which are available in the sensory input and can in principle be used to obtain an estimate of POC which is adequate to solve the collision task [e.g., depth perception, Gray and Regan (1998) and Cavallo and Laurent (1988); size and motion based information, DeLucia and Warren (1994); see also review Zago et al. (2009)]. However, it is much less clear on what visual information subjects do actually rely in order to avoid collisions with objects in the path of motion and how this information is selected when various sources are present? Here, studies are needed indicating the relevant environmental cues and the mechanisms of selecting these cues from the sensory input. Suitable attempts in understanding such search and identification behavior will include the analysis of gaze movements associated with detection of relevant visual stimuli and directing attention. Overall, it seems clear that gaze does play an important role relevant in obstacle since more than 90% of traffic accidents are due to problems with the acquisition of visual information (e.g., Sivak, 1996). To date just a few studies are published analyzing attentional processes in multiple-object collision detection (Andersen and Kim, 2001; Vaux et al., 2010). Additionally, less attention was given to gaze movements in service of gathering relevant information from the multiple collision events. In the present paper, we provide studies which combine the presentation of multiple moving (and collision relevant) objects with the measurement of gaze movements in a traffic intersection task.

HYPOTHESES ABOUT THE ROLE OF GAZE AND SPATIAL MEMORY IN COLLISION AVOIDANCE

As mentioned before, the main emphasis in studies of obstacle avoidance behavior has been on sensory cues (e.g., retinal flow patterns) and their bottom-up processing. With bottom-up processing visuo-motor control can proceed without awareness (pre-attentively), which is probably the normal mode regarding fast and skilled interceptive actions, i.e., interceptive actions bypass cognitive operations. More recently, the key role of prior knowledge (i.e., priors related to temporal and spatial characteristics of the physical world) and internal models (i.e., top-down processing) associated with the allocation of attention for guiding interceptive behavior has attracted increased interest (Land and McLeod, 2000; Andersen and Kim, 2001; Wickens et al., 2001; Zago et al., 2004; Dessing et al., 2005; Jovancevic et al., 2006; López-Moliner et al., 2007; Mrotek and Soechting, 2007; López-Moliner and Keil, 2012; Diaz et al., 2013). Collision avoidance in dynamic environments involves the scanning of many potentially relevant obstacles, only a few of which are selected for tracking. It seems plausible that this process is based on three components; information intake by sensory processes, motion planning, and risk anticipation in a working memory stage, and the interaction of these two in attention and sensory-motor control. In this article, we will address these components.

In a series of experiments, we tested the following hypotheses and predictions: (1) Gaze patterns are adapted to the task of collision avoidance but do not predict the performance of individual subjects or trials (section Gaze Behavior in the Traffic Intersection Task). (2) The representation of cars within spatial working memory is task specific, i.e., cars with high POC are remembered better

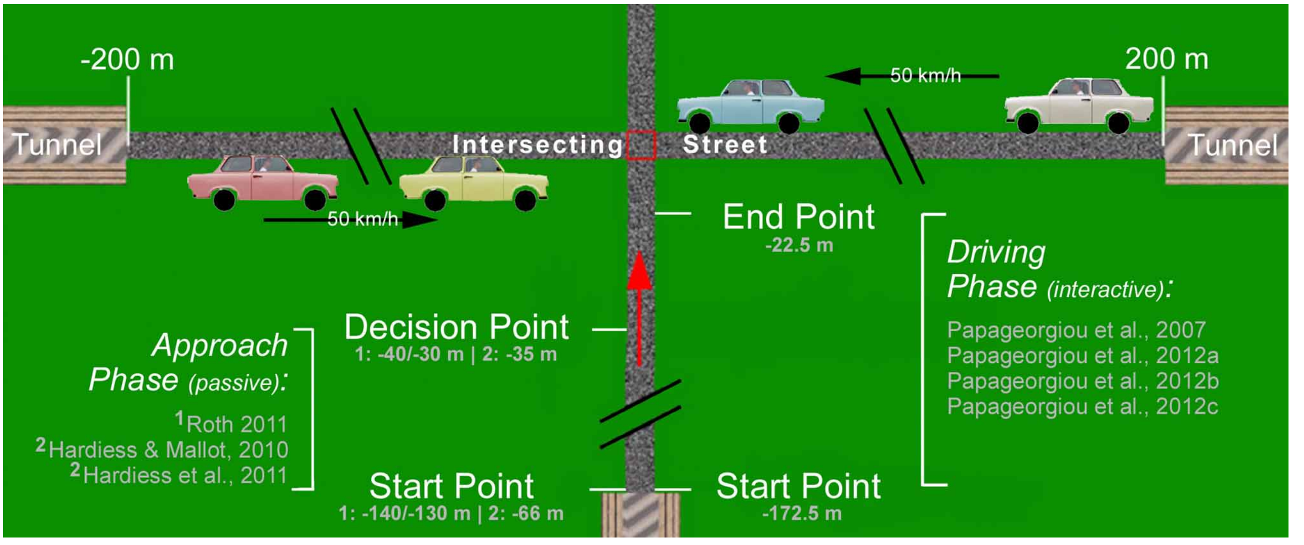

FIGURE 1 | Overview of the traffic intersection experiments used to analyze the function of gaze and visuo-spatial memory in the task of collision prediction or avoidance in normal and visually impaired subjects. The overall structure of the intersection task used in all our experiments was as follows: beginning from a start point, subjects approached (passively or interactively, i.e., controlling their speed) the intersection while visually observing of the traffic on the intersecting street in order to predict or avoid a collision. The cars on the intersecting street had different colors and were uniformly distributed over two lanes (right-hand traffic); their number could be varied to allow for different traffic densities. The speed of the traffic cars was always constant with 50 km/h and their travel paths started and ended in tunnels. In passive trials, subjects approached until a decision point where estimates about a collision or the positions of traffic cars were made. In interactive trials, subjects were allowed to adjust their own driving speed (within certain limits) within the approach section between the start and end points marked in the figure. From there on, movement was extrapolated with constant speed and the occurrence of collisions was recorded.

(ranked higher) than cars with low POC (section Allocation of Spatial Working Memory). (3) We predict that working memory processes are crucial for selecting cars with the most significant POC in street crossing. Consequently, subjects with working memory disorders should fail in collision avoidance. To test this hypothesis we investigated gaze patterns and collision avoidance in stroke patients showing similar visual field defects but differ in working memory function (section Role of Gaze and Working Memory in Visually Impaired Subjects).

EXPERIMENTS ABOUT COLLISION AVOIDANCE

EXPERIMENTAL PARADIGM—THE TRAFFIC INTERSECTION TASK

This section summarizes a series of experiments investigating gaze scanning strategies and their interactions with working memory for the purpose of obstacle detection and avoidance in a dynamic environment. To test subjects in a "real-world" scenario under controllable conditions, a virtual intersection task was developed where visually impaired as well as healthy subjects were required to detect and avoid collisions while approaching and crossing a street with two-directional traffic (see **Figure 1**). A driving simulator was used for all experiments (**Figure 2**). Eye and head tracking was combined to a gaze vector comprising azimuth and elevation of joint head and eye directions in a lab-based frame of reference. The approach to the intersection was along a straight road with prescribed or self-controlled speed, but with no additional traffic, traffic signs, or curves. Thus sensory motor tasks such as steering, checking the rear-view mirror, looking out for road signs, other vehicles, or pedestrians, as well as gear shifting were excluded. Attentional actions are therefore restricted to monitoring the crossing traffic, including the selection and monitoring of cars considered as possibly threatening a collision. Such cars are relevant for the task of adjusting the own

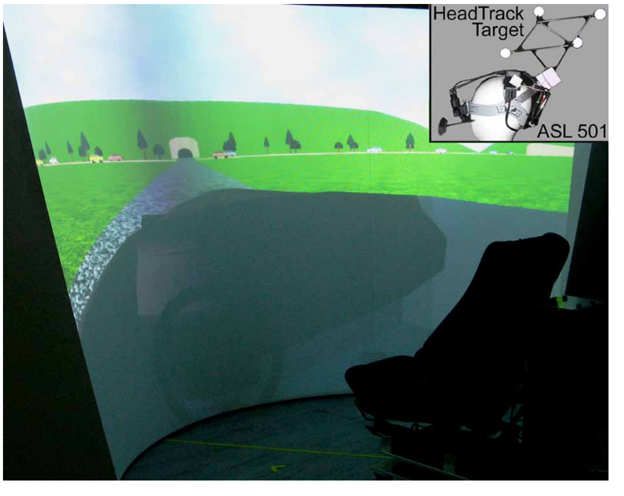

FIGURE 2 | Large-field projection screen (presenting the approach phase of the experiment) and seat used in the experiments. The screen provides a large field of view of 150 by 70° in a seated but otherwise unrestricted subject. Inset: eye and head tracking devices with 60Hz sampling frequency (head: ARTtrack/DTrack from A.R.T., eye: model 501 from Applied Science Laboratories).

velocity in order to hit a gap in the crossing traffic. Thus, by presenting two streams of potentially hazardous cars (rather than just one intercepting object) we extend the task of time-to-collision estimation to the process of sampling and selecting collision relevant items. Consequently, subjects are required to constantly engage in two processes, first, sampling and representing the traffic scene in an adequate way (i.e., in terms of task relevance) and second, calculating and predicting POC for selected cars in order to generate appropriate behavior.

ROLE OF GAZE AND SPATIAL MEMORY IN SUBJECTS WITH NORMAL VISION

Gaze behavior in the traffic intersection task

A non-interactive version of the traffic intersection task was used to investigate the role of gaze movements in collision avoidance (Roth, 2011). Specifically, we addressed the question whether individual gaze movements or more complex gaze patterns are predictive for task performance (i.e., collision detection). In a variety of comparable trials, 25 healthy subjects were passively watching an approach to the intersection (see **Figures 1**, **2**) with one of eight traffic configurations (four of which would entail a collision). Before reaching the crossing, the display stopped and all cars were hidden. The subjects then had to decide if they would pass the crossing without a collision or not.

Traffic situations were derived from two basic arrangements with a total of 19 cars driving in both directions. One of these cars would cause a collision if the approach would have been continued to the intersection. To avoid learning effects while repeatedly confronting a subject with one and the same traffic situation, the two traffic situations were mirrored and car colors were changed in a random fashion in each trial. This results in four traffic scenarios with a collision relevant car (i.e., hit or miss trials) and four additional collision-free conditions (i.e., correct rejection or false alarm trials) generated by simply removing the relevant car. All traffic cars had the same constant speed of 50 km/h. During the approach phase (length: 100 m; duration: 9 s), subjects passively drove toward the intersection with a constant speed of 40 km/h (**Figures 1**, **2**). Two different start and decision points (140/40 m and 130/30 m in front of intersection) were assigned randomly to the trials. At the decision point, the remaining distance to the intersection was therefore 40 or 30 m, respectively. Each subject performed 80 trials, 40 with a collision relevant car and 40 without, in randomized order. At the decision point all cars were hidden (time-to-collision of the collision relevant car at the time of hiding was 3.6 or 2.7 s, respectively) and the subject was ask to answer the question "would you cause a collision assuming that the approach proceeds with the same speed?" with "yes" or "no." After answering the question a feedback (crash "yes" or "no") was given to the subject.

The overall task performance (i.e., percentage of correct judgments of the subjects) was high, i.e., the average of d-prime values [$d' = z(\text{Hit}) - z(\text{FalseAlarm})$; Swets, 1996] was significantly above zero (**Figures 3A,B**). Hit rate per subject ranged from 20 to 100% while false-alarm rate varied only between 5 and 55%; only two subjects showed false-alarm rates above 50% for no-crash trials (**Figure 3A**). D-prime values were significantly above zero ($P < 0.05$) according to Marascuilo's one-signal test (Marascuilo, 1970) for 14 out of 25 subjects. Subjects' performance differs with respect to both, d-prime and criterion values. The criterion C was calculated to detect any observer bias ($C = -0.5 \times [z(\text{Hit}) + z(\text{FalseAlarm})]$). The averaged bias (**Figure 3B**) was slightly positive indicating a tendency toward

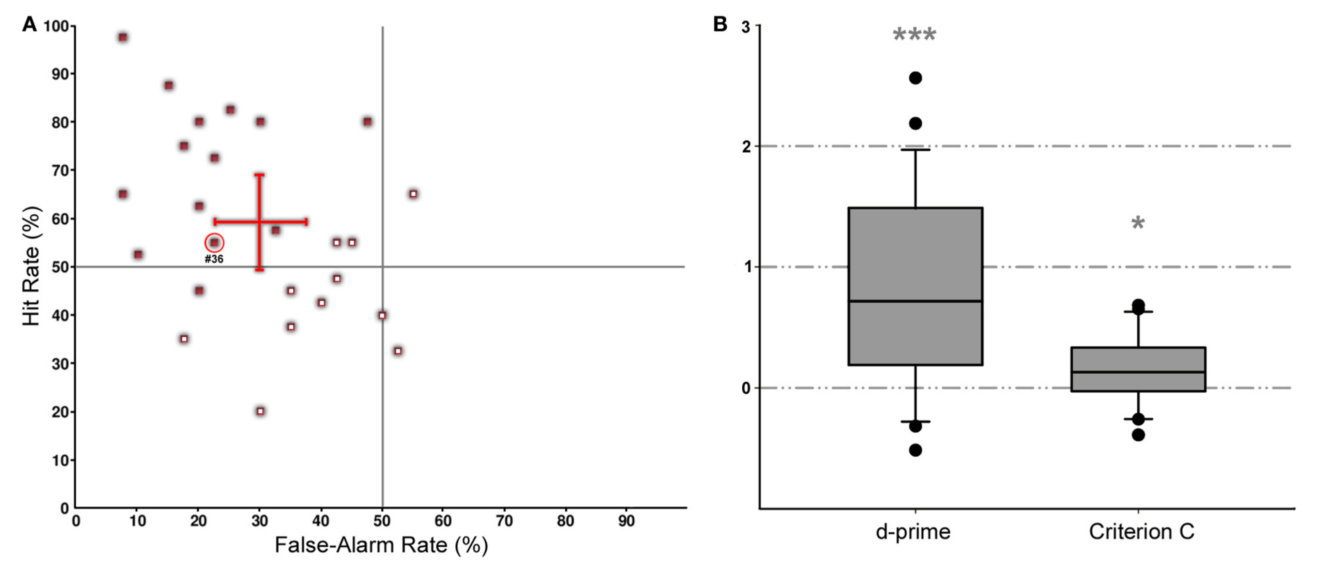

FIGURE 3 | Collision detection performance. (A) Distribution of individual hit and false alarm rates shown for all 25 subjects (red squares). Data points significantly different from zero are marked by open symbols. Values for the mean and standard deviation of the hit (value: 59 ± 20%) and the false alarm rates (value: 30 ± 14%) are depicted as a red cross. The red circle denotes that subject (#36) for which scan-path details are shown in **Figure 4**. **(B)** Box plots of the averaged discriminability index (d-prime; left) and the averaged criterion for an observer bias (C; right). Statistical effects (one-sample *T*-Test, test value: zero) are presented for criterion C and d-prime (*$p < 0.05$; ***$p < 0.001$).

"no" responses (i.e., a more conservative performance—in case of doubt subjects will rather say that no crash will occur). Note that an undetected crash resulted simply in the presentation of a "crash sign" with no further consequences for the subject.

The collision detection task requires the assessment of the POC of 19 (initial number, cf. **Figure 4B**) individual cars appearing at the onset of the experiment. Possible strategies for selection, scanning, and POC estimation can be inferred from the subjects' gaze patterns performed during the 9 s approach phase. The overall gaze pattern we found was determined by an initial shift to the left followed by a shift to the right side within the first 6 s (cf. **Figure 4**). During the last 3 s, additional left-right oscillations are noticeable. The initial left-right-left pattern occurring in most of our subjects was assumingly due to a well-trained and habituated gaze behavior on streets with right-hand traffic. Besides this global gaze pattern, local oscillations also occurred allowing to sample and select the most relevant cars regarding their POC (**Figure 4**).

In addition to this global scanning behavior, two more task-specific properties of gaze behavior can be observed. First, only cars moving toward the intersection ("inwards") are taken into consideration while cars that have already passed the intersection

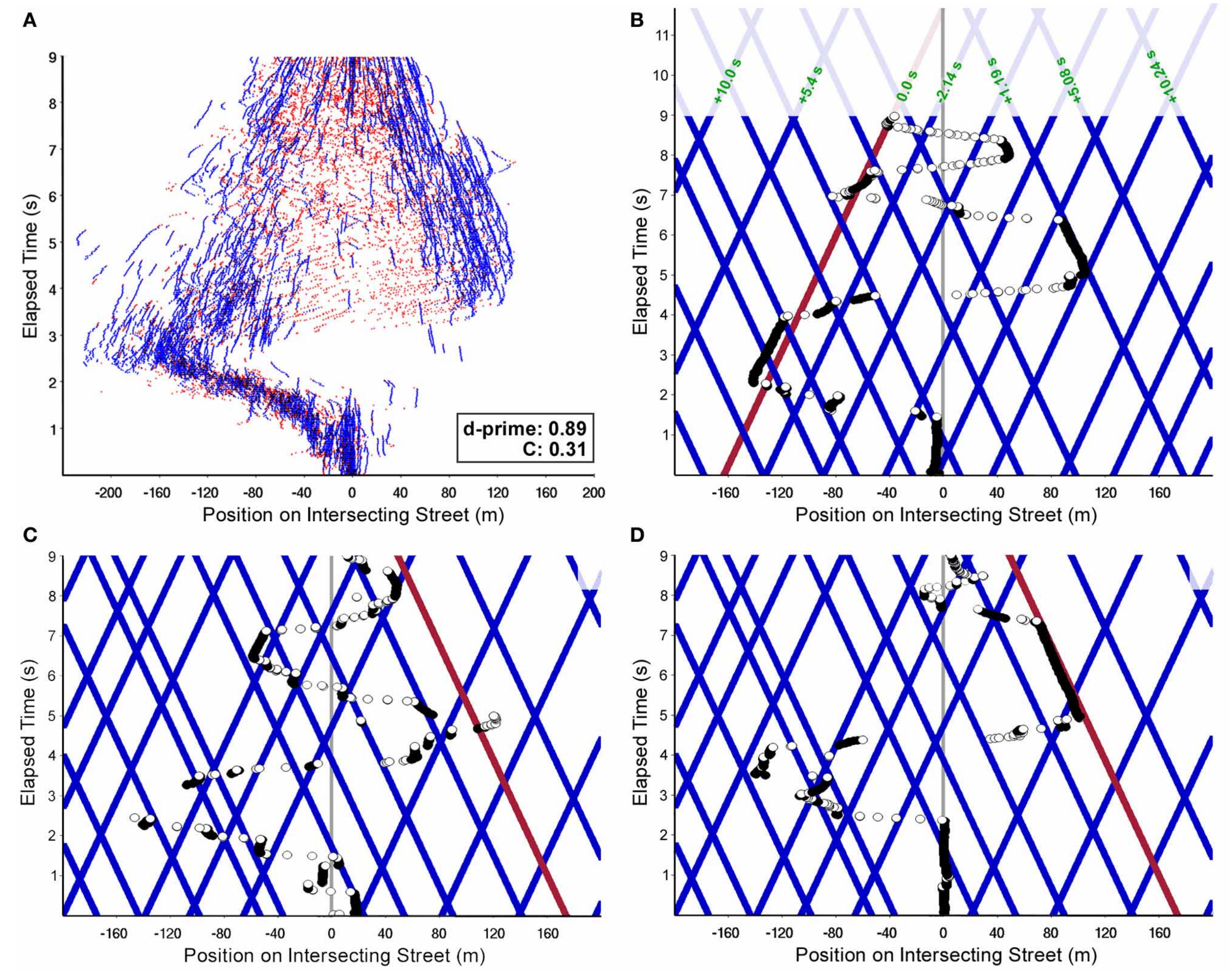

FIGURE 4 | Scan-path examples of a representative subject (#36; hit rate: 55%, false-alarm rate: 22.5%; see Figure 3A). (A) Gaze scan-paths for all 80 trials performed by the subject are plotted together. Blue parts of the scan-paths denote fixations and red ones saccades. The left-right-left pattern of gaze movement combined with local scanning was found as general pattern in all subjects. Note the inward slant of the blue segments, indicating that object fixations almost exclusively landed on to cars approaching the intersection (d-prime and observer bias are reported for this subject). **(B)** Exemplary scan-path of the approach to the intersection for a single hit trial. The positions of all cars over time are shown in blue; the collision relevant car is depicted in red, i.e., the red line hits the subjects' trajectory (vertical midline) at time 11.7 s. Position lines of all cars after the time the cars disappear are drawn with transparency. Fixational elements of the gaze scan-path are drawn as black, positions during saccades as white circles. Differences in time-to-collision for all cars with relevant POC are given relative to the colliding one (numeric values in green). **(C)** Another exemplary scan-path of the approach to the intersection for a hit trial where no relevant fixations to the colliding car occur. **(D)** Exemplary scan-path of the approach to the intersection for a single miss trial. Please note, despite fixating the collision relevant car for about 2 s, the subject failed to detect the high POC of that car.

point are ignored. This can be seen from **Figure 4**, where almost all fixational segments of the scan-paths are slanted inwards. That is, although cars driving in both directions were visible at each position along the intersecting street, subjects clearly select the cars with larger POC. Second, in terms of eccentricity, cars with high POC will occur around positions $x_c = z \times v_c/v_s$, where x_c is the distance of the car from the intersection, z the subject's distance from the intersection, and v_c, v_s are the velocities of the intercepting cars and the subject, respectively. In **Figure 4**, traces of cars approximately satisfying this condition are shown in red. As is best visible from **Figure 4A**, the distribution of fixation targets clearly peaks around the visual direction with highest POC. Taken together, both selection mechanisms generate a spatio-temporal pattern of the allocation of attention summarized in **Figure 5**.

The overall attentional resource which must be allocated adequately to the traffic cars is thought to be fixed and limited (i.e., only about four items can be simultaneously represented in working memory, e.g., Brady et al., 2011). Furthermore, we assume that subjects shifted their attention in an overt fashion, i.e., shifts of attention are associated with gaze movements [cf. shift of attention toward foveal vision in complex traffic stations: Miura (1987) and Crundall (2005)]. At the beginning of the approach, a substantial amount of attention should be allocated to cars in the far periphery of the intersection (**Figure 5**, blue curve). In this early stage, attention can be allocated broadly and with low amplitude (i.e., intensity) because the actual POC is relatively small as long as the intersection is distant. During the approach, the attention is zooming in to the margins of the intersection and ends up as a localized, high amplitude peak (**Figure 5**, orange curve). Here, the relevant time window is very small and POC considerations concern only one single position of possible colliding cars.

Figures 4B,C shows a typical scan-path of a single approach for a crash trial (colliding car in red). The overall scanning is shaped by the global left-right-left pattern (cf. also **Figures 4A,D**). Additionally, a pattern of shifting attention overtly as illustrated in **Figure 5** is obvious. During scanning, fixations with short duration are applied to cars in order to sample for their possible POC (selection). Long lasting fixations are directed to selected cars (two cars in **Figure 4B**), presumably to estimate their actual POC. Such estimates of POC can be obtained by two strategies (i.e., image-based and memory-based). In an image-based approach, image-expansion (processes based on *tau*; see section Bottom-Up Processing and Mechanisms for Interceptive Actions) as well as object bearing are processes that might be involved in estimating the POC (cf. Andersen and Kim, 2001). Object bearing [i.e., the angle between the heading and an intercepting car, $\tan^{-1}(v_c/v_s)$] can be measured over a range of time. Cars with high POC will have bearing shifts, which are close to zero (constant bearing angle strategy; see section Bottom-Up Processing and Mechanisms for Interceptive Actions). Here, bearing could be based on retinal (without gaze-shifts) or extra-retinal (gaze shifts are possible and object positions must be updated in a visual array) representations. In any case, the constant bearing strategy will work only if the observer and objects translate at constant velocities and along linear trajectories. Indeed, these requirements were met in our experiment. However, in a similar experiment with variable relative speed of object and observer, subjects applied similar and comparable gaze patterns (cf. **Figure 8** and Papageorgiou et al., 2012c). In addition, Andersen and Kim (2001) found in collision detection experiments where multiple objects were present only small interference effects concerning the bearing angle. In conclusion, we cannot completely rule out the possibility of relying on an image-based representation. However, the exclusive use of such a format seems unlikely.

Dealing with multiple targets and keeping track of trajectories over time requires a working memory allowing to store the relevant parameters for each target. This storage might be a simple list of the sensory data obtained for each object, but allows to integrate incoming data with previously stored data of the

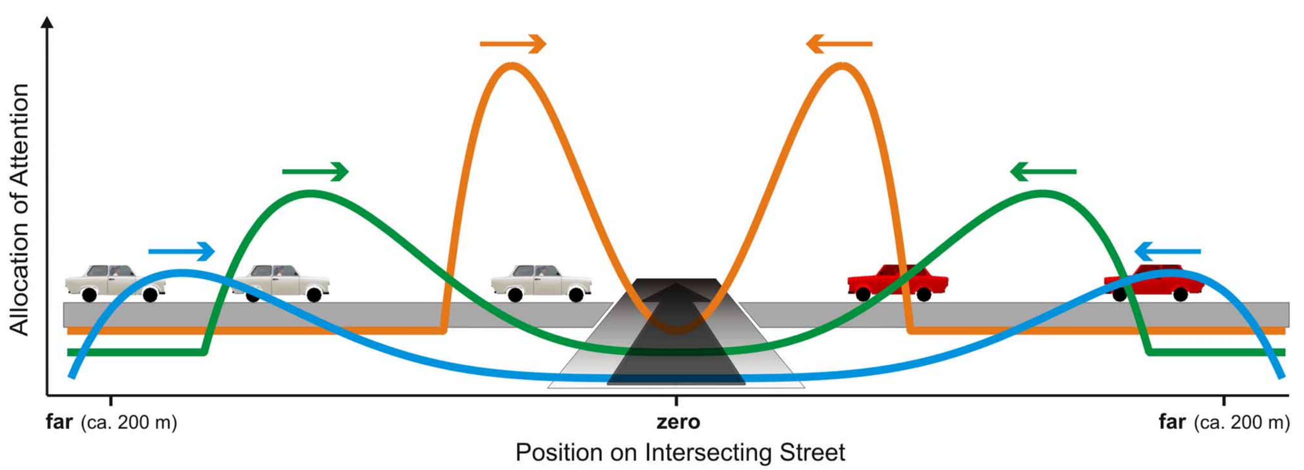

FIGURE 5 | Schematic account of the allocation of overt attention (i.e., distribution of fixations) during the approach to the intersection is scaled by the subject's distance to the intersection (blue: furthest, green: intermediate, and orange: closest) combined with the position of the traffic cars. Additionally, only cars moving toward the intersection are considered (arrows).

same object, as well as extrapolation of future states. One could also think of this working memory as an ego-centric "mental" map featuring object position and trajectories, where the frame of reference is given in optic flow variables such as nearness (distance over ego-speed), bearing, etc. The raw data that this map is based on is the same as in the image-based case, the difference of the two approaches being the presence of a working memory component.

If working memory is involved, distance can also be judged from the image size of the cars and prior knowledge about car sizes. The estimation of distance based on familiar size has been found also for other tasks, such as the interception of free-falling objects (Tresilian, 1993; Peper et al., 1994; Wann, 1996). The phenomenon of speed constancy, where the speeds of two objects located at different distances but moving physically with the same speed, are perceived as equal, accounts also to this idea of relying on familiar size (Palmer, 1999; Distler et al., 2000). Note that an internal model of known size need not be considered as a cognitive, declarative parameter (López-Moliner et al., 2007). It may rather result from a process of calibration in which subjects learn, through experience, to adapt their internal representation.

The built-up of a working memory over time is likely related to the pattern of gaze movements. Repeated or prolonged fixation or tracking of a target will improve the accuracy of image-based measurements and therefore the working memory representation. In this sense, gaze movements may contribute to speed estimation in depth, vertical elevation, and horizontal azimuth (e.g., Brenner and Smeets, 2011; Spering et al., 2011). Smooth pursuit can be accurate to within 5% for target speeds up to about 57°/s (Bahill and McDonald, 1983). Bennett et al. (2007) found that subjects can estimate the acceleration of a temporarily occluded object by the use of smooth and saccadic eye movements. Our data indicate that subjects use many but brief fixations to gain an overview of the most relevant cars, while a small number of long lasting fixations are used for the POC calculation of the selected cars. We conclude that a working memory of the described type (i.e., some sort of local "mental map") is involved in these processes.

Subject's gaze behavior is clearly adapted to the visual presentation and the task. It therefore seems plausible to assume that a correlation exists between the gaze pattern in a given task and the performance. However, no such correlation was apparent from our experiments employing extensive analyses of relevant gaze parameters. As an example, **Figure 6** shows the distribution of the landing points of all fixations for one traffic situation. The distribution for good performing subject is slightly more focused on the intersection point, but the differences are not large enough to allow a prediction of collision detection performance from gaze pattern.

One gaze parameter that seems to be slightly predictive of task performance is re-fixation rate. While overall, re-fixation rate for the collision relevant car is rather low (about 30%), subjects performed significantly more re-fixations on that car in hit trials as compared to miss trials. In addition, re-fixations were more likely to occur during the second half of the approach (from 4.5 to 9 s).

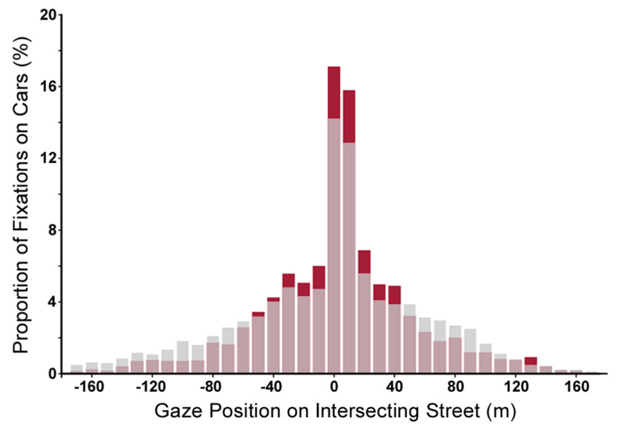

FIGURE 6 | Distribution of task relevant fixations applied in all crash trials shown as proportion of fixations on cars (during the approach) for good performers (subjects with hit rates above 50%, red bars) and for poor ones (subjects with miss rates above 50%, gray bars). Redrawn from Roth (2011).

Allocation of spatial working memory

Independence between gaze behavior and task performance in collision avoidance was also reported by Hardiess and Mallot (2010). In this study, a modified version of the collision avoidance paradigm (**Figure 1**) was used to investigate how well each car is represented in working memory. Here, subjects passively approached the intersection up to a certain point where the approach stopped and all traffic cars disappeared. Then, subjects were required to reconstruct from memory the last traffic configuration as seen at the time of stopping. For the reconstruction task, images of cars heading left and right were presented in the upper part of the display screen. Subjects used a joystick to drag and drop these cars to the remembered positions on the intersecting street. The placement positions were recorded in each trial. **Figure 7A** shows summary results for the position and heading direction of placed cars. Cars driving rightwards are mostly placed left of the intersection while cars driving left are placed predominantly on the right side. Thus, cars with high POC are remembered better than cars with low POC. This may be due to selective information take-in as demonstrated in **Figure 4**, to selective memory formation in working memory, or to both of these effects.

Task specific working memory representation was also revealed in a change detection version of the traffic intersection task conducted by Hardiess et al. (2011). Here, during the approach subjects had to observe different traffic situations in preparation of collision avoidance. In a subset of trials, the approach stopped before reaching the intersection. After a short delay (330 ms) during which the screen was turned blank, a traffic configuration was displayed which either equaled the final arrangement at stopping, or differed by removal of individual cars at various positions along the intersecting street. Subjects were then requested to report recognized differences between the presented configuration and the configuration at the end of the (interrupted) approach phase (i.e., change detection task).

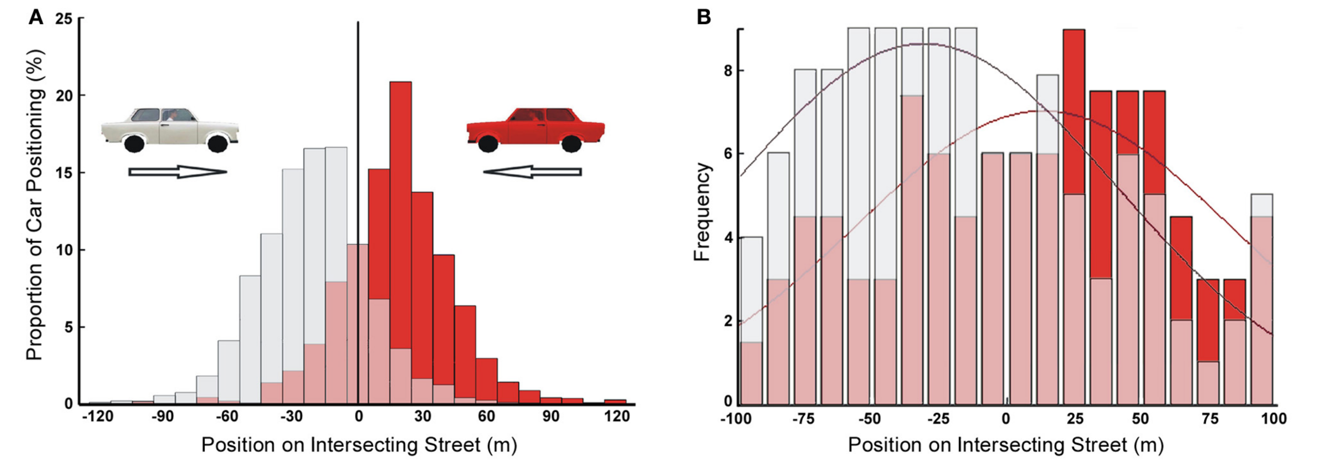

FIGURE 7 | Task specific representation of cars in working memory shaped by their POC (gray: cars moving from left to right; red: cars moving from right to left). (A) Distribution of number of cars positioned on the intersection in the memory recall phase (i.e., reconstructing the traffic scene) of the traffic intersection task [redrawn from Hardiess and Mallot (2010)]. **(B)** Frequency of correct detection of change due to cars removed from all positions on the intersecting street (i.e., only hit trials are considered) in the change detection version of the traffic intersection task [redrawn from Hardiess et al. (2011)]. The smooth curves show normal distributions fitted to the data.

Figure 7B shows the frequency of correct detections as a function of car position and driving direction. While the distributions are broader than in the previous experiment, the advantage of cars approaching the intersection (i.e., cars with high POC) is clearly apparent.

In conclusion, gaze patterns were not found to be predictive of task performance, i.e., we found almost the same gaze behavior regardless of whether collisions were predicted correctly or not (cf. also **Figures 4B,D**; similar gaze pattern despite different performance). However, during the processes of visual perception ending in the representation in spatial working memory cars were weighted based on their POC. These results together with the fact that subject's performance varies substantially, indicate that subjects must differ in the mental processes of representing the equally selected (by means of gaze) material within spatial memory. Such variations could be related to differences concerning executive functions, capability of working memory, or learning ability.

ROLE OF GAZE AND WORKING MEMORY IN VISUALLY IMPAIRED SUBJECTS

In this section, we report findings about collision avoidance in patients with homonymous hemianopia regarding their ability to recruit gaze as well as memory resources to compensate the visual field loss. Hemianopic scanning is primarily visually elicited, i.e., patients with homonymous visual field defects (HVFDs) can be seen as a kind of model for visual exploration under low vision. In order to underline the role of active vision in the patients' compensational behavior, data about demographic and clinic factors are presented and shown to be not predictive of collision avoidance performance. Rather, functional gaze adaptation in combination with spared working memory capacities enables a subgroup of patients to adequately compensate their visual field loss.

Collision avoidance in persons with homonymous visual field defects (HVFDs)

Patients with HVFDs are impaired by a binocular restriction of the visual field caused by unilateral post-chiasmal brain damage due to cerebrovascular accident, traumatic brain injury, or tumors (Zihl, 1994, 2000; Kerkhoff, 1999). Depending on magnitude and site of the lesion, HVFDs can comprise small scotomas, loss of one visual quadrant, or larger losses affecting up an entire visual hemifield (half side loss). HVFDs create a marked amount of subjective inconvenience in everyday life (Papageorgiou et al., 2007; Gall et al., 2009). Patients with HVFDs may show impairments of reading, visual exploration and navigation, collide with people or objects on their blind side, and may be deemed unsafe to drive (Trauzettel-Klosinski and Reinhard, 1998; Zihl, 2000). This has led to the belief that homonymous visual field loss is *per se* associated with functional impairment.

Driving has been considered to be problematic for patients with HVFDs and investigations concerning the performance of hemianopics in realistic or simulated driving report a variety of findings. The majority of studies have highlighted poor steering control, incorrect lane position, and difficulty in gap judgment as the primary problems of drivers with HVFDs (Szlyk et al., 1993; Tant et al., 2002b; Bowers et al., 2009, 2010; Wood et al., 2009). Further, in an interactive version of the traffic intersection task, Papageorgiou et al. (2012a) studied one of the core abilities in driving—collision avoidance—in 30 patients with HVFDs (20 with hemianopia and 10 with quadrantanopia) and 30 normal-sighted group-age-matched controls. In a large number of trials, subjects had to actively (i.e., continuous adjustment of the own speed between 18 and 61 km/h by means of a joystick) hit a gap between cars moving on an intersecting street (cf. **Figure 1**). In two experimental conditions, the density of traffic cars was adjusted to achieve two different collision probabilities, i.e., 50 and 75%, respectively. When analyzing all patients together, subjects with HVFDs had on average more collisions than subjects with normal vision. The difference between the controls and patients was about one more crash for 50% density and two more crashes for 75% density. In density 75%, hemianopics experienced more collisions with vehicles approaching from the blind side than the seeing side. Additionally, in density 75%, the number of collisions on the seeing side of subjects with HVFDs was similar to the number of collisions experienced by normal subjects. In the easier task (density 50%), differences in collision rates between the blind and seeing hemifield were not obvious. These results suggest that patients with HVFDs were less efficient and experienced difficulties in collision avoidance when intersecting a traffic street. In a further analysis (Papageorgiou et al., 2012c) we subdivided the collective of HVFD patients based on the number of collisions caused in 50 and 75% density trials. Thus, the splitting involved a joined performance measure for the two tasks of different difficulty and resulted in two subgroups (adequate: $HVFD_A$ and inadequate: $HVFD_I$) each one consisting of 15 patients. $HVFD_I$ patients still showed reduced collision avoidance as compared to healthy controls for both traffic densities. In contrast, the subgroup of $HVFD_A$ patients showed performance values identical to controls for both densities and for crash number as well as trial duration. This result, i.e., that the adequate subgroup of patients performed similar to controls, was also shown for other visual tasks (Zihl, 1999; Machner et al., 2009; Hardiess et al., 2010) indicating that some patients compensate functionally for the visual impairments while others do not or not to a sufficient amount.

Concerning visual exploration and collision avoidance it has been a matter of debate whether driving performance of patients with longstanding HVFDs is primarily determined by visual field parameters (e.g., the extent of the visual field along the horizontal meridian, Johnson and Keltner, 1983; size of the area of sparing within the affected hemifield, Papageorgiou et al., 2007), or affected by additional factors, such as age of patients, side of brain injury, time span since lesion onset, and compensation by adapted gaze and memory strategies (Pambakian et al., 2000; Papageorgiou et al., 2007; Hardiess et al., 2010; Wood et al., 2011). Papageorgiou et al. (2007) investigated the correlations between visual field measures and the collision avoidance performance in the interactive traffic intersection task as well as a vision-targeted and health-related quality of life score (i.e., NEI-VFQ-25) in a large population of 33 HVFD patients. Interestingly, neither collision avoidance nor performance in everyday life was found to correlate significantly with the extent of visual field loss. In a follow-up investigation, side of brain injury and time span since lesion onset could be excluded as factors influencing collision avoidance performance (Papageorgiou et al., 2012a). Under the tested clinical and demographic variables, the age of the patients was the only variable correlated with task performance (the older the patients the higher the crash rate). However, an effect of age on performance was also found for the age-matched healthy controls. In conclusion, it can be argued that clinical and demographic factors play just a minor role in explaining the variability of hemianopics in driving tasks (as well as in tasks that demand visual functions to a lower extent; cf. Hardiess et al., 2010). Rather, functional compensation of the HVFDs by applying adequate eye and head movements in combination with intact spatial memory will help the patients to overcome their limitations and to reach task performance in the range of healthy subjects.

Role of gaze and working memory for visual field compensation in collision avoidance

Studies with patients suffering from binocular visual field deficits (i.e., HVFDs) are instrumental in assessing the gaze strategies and their adaptation to reduced information intake (i.e., hemianopic scanning is primarily visually elicited, namely by the visual defect and not by additional brain damage; Tant et al., 2002a) and maybe reduced processing capacities (Papageorgiou et al., 2012b). As compared to healthy subjects, patients' strategies may differ with respect to scan-path pattern and memory involvement, leading to various levels of functional compensation. In the following sub-section, we review evidence for the hypothesis that gaze adaptation is the primary compensatory mechanism in patients with HVFDs to achieve collision avoidance, but that in addition to gaze adaptation, the availability of working memory capacities must also be considered.

From studies investigating visual exploration, it is known that patients with HVFDs are able to behave adequately compared to healthy subjects by applying compensatory gaze movements. In general, when viewing simple horizontal line patterns or line drawing, hemianopics spend most of the time looking toward their blind hemifield in order to bring more of the visual scene into their seeing hemifield (Ishiai et al., 1987). Such displacement of the fixation point toward the hemianopic side was considered to be an efficient compensatory strategy and was observed in numerous other basic tasks, including dot-counting (Zihl, 1995; Tant et al., 2002a; Hardiess et al., 2010), viewing of natural and degraded images (Pambakian et al., 2000) and visual search (Hardiess et al., 2010). Papageorgiou et al. (2012c) investigated gaze compensation of hemianopic patients in a more demanding task, i.e., the interactive traffic intersection task under dynamic and time-constrained conditions. In this task, participants (14 HVFD patients and 19 controls) were confronted with 30 different traffic situations presented in two traffic densities. The task was to adjust own driving speed to avoid any collision with a traffic car, i.e., to hit a gap in the crossing traffic [for task details see section Collision Avoidance in Persons with Homonymous Visual Field Defects (HVFDs), study by Papageorgiou et al. (2012a), and **Figure 1**]. To introduce a time-constrained situation, participants were not allowed to stop their driving at any point in time. Regarding their collision avoidance performance we divided the collective of patients in two subgroups [five adequate: $HVFD_A$ and nine inadequate: $HVFD_I$ patients; cf. section Collision Avoidance in Persons with Homonymous Visual Field Defects (HVFDs)].

In order to identify gaze strategies associated with successful collision avoidance, relevant gaze-related parameters were analyzed as a function of participant group ($HVFD_A$ patients, $HVFD_I$ patients, and normal subjects) for traffic density 50 and 75%. Normal subjects and $HVFD_A$ patients shared many similarities regarding their gaze patterns and differed in parameters regarded as relevant for functional compensation. In both densities, no differences were found for number of fixations, fixation duration, scan-path length, and number of gaze shifts (between the left and right side of the intersecting street). However, $HVFD_A$ patients went to larger gaze eccentricities and made more fixations on cars, presumably resulting in a good estimate of the POC and successful collision avoidance. Additionally, a higher proportion of fixations and gaze eccentricity, and shorter saccades to the blind hemifield were evident for $HVFD_A$ patients. Interestingly, $HVFD_A$ patients displayed increased gaze eccentricity (i.e., more scanning activity) especially in the first and middle part of the approach, which indicates the importance of gaining an initial overview of the scene (see **Figures 8A,B**). In summary, $HVFD_A$ patients displayed distinct gaze patterns characterized by an overall increased exploration, particularly toward moving objects of interest on their blind side, to adapt successfully to their visual deficit. This compensatory behavior becomes especially evident during the more demanding task, i.e., the high traffic density condition.

On the other hand, $HVFD_I$ patients exhibited gaze patterns completely distinct from normal subjects. All examined gaze-related parameters (except for number of fixations and fixation duration) were significantly different between the two subgroups of patients and illustrated a decreased and unorganized visual exploration of $HVFD_I$ patients (cf. **Figures 8A,C**). Compared to normal subjects, these differences may explain the failure of compensation in $HVFD_I$ patients.

In conclusion and to bring the findings from Papageorgiou et al. (2012c) together with other studies about functional compensation (Zihl, 1995, 1999; Schuett et al., 2009; Hardiess et al., 2010), patients classified as adequate (in order to compensate for the visual field defect) are able to use different compensatory gaze strategies, which are gradually intensified as task complexity increases. Compensational gaze scanning led to a more efficient (superior) fixation pattern for $HVFD_A$ patients, providing more fixations on cars than $HVFD_I$ patients (and healthy controls). This strategy resulted in a better identification of the collision-relevant vehicles and successful (adequate) collision avoidance.

Besides visual field deficits, HFVD patients have been shown to suffer from brain lesions in regions commonly associated with visuo-spatial memory (Machner et al., 2009; Hardiess et al., 2010; Papageorgiou et al., 2012b). In these studies, inadequate patients were found to show larger lesions than adequate patients, especially in mesio-ventral areas of the temporal lobe (i.e., the fusiform gyrus), the inferior occipital lobe, and the para-hippocampal gyrus. In some $HVFD_I$ patients, the right posterior parietal cortex or left parietal regions were affected. Temporal regions belong to the ventral processing visual stream, thought to be involved in objects recognition (Ungerleider and Mishkin, 1982) and may also play a role in the control of attention (Goodale and Milner, 1996; Ungerleider and Pasternak, 2004). Disturbance of attentional modulation within the ventral processing stream and damage of its connections with temporal lobe areas and the prefrontal cortex might be impair visuo-spatial memory. Since the para-hippocampal gyrus serves as the main pathway between the hippocampus and cortical association areas, its damage can

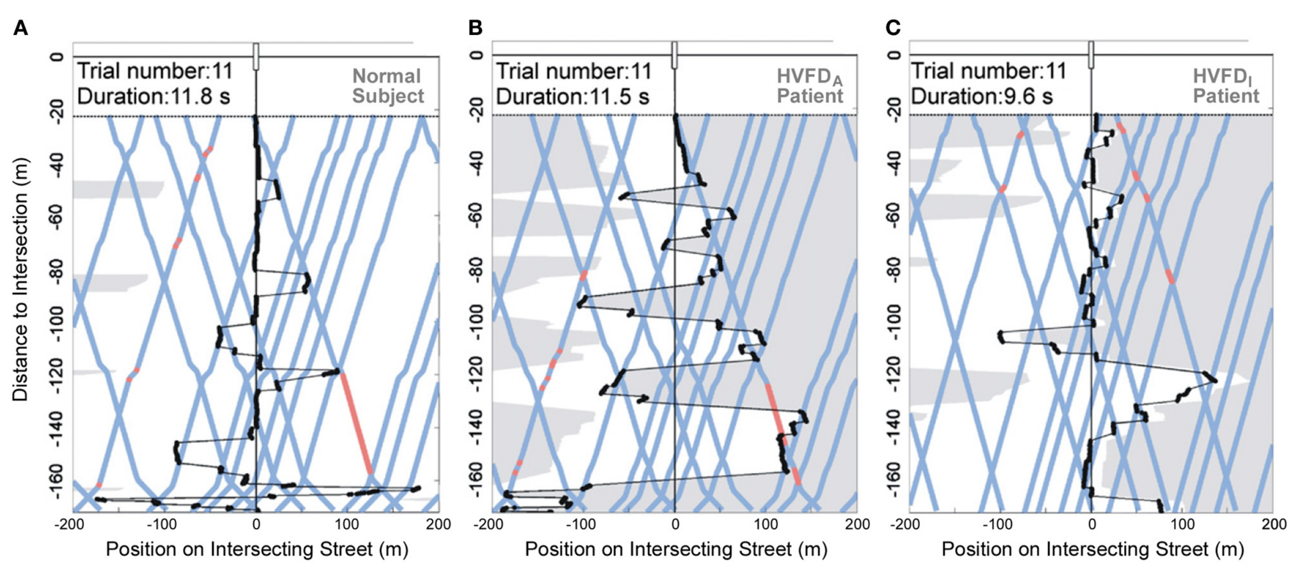

FIGURE 8 | Visualization of gaze trajectory. Each plot demonstrates the participant's gaze pattern during approach to the intersection for a representative trial with 50% traffic density. A normal subject **(A)**, an adequate-$HVFD_A$ patient with right hemianopia **(B)**, and an inadequate-$HVFD_I$ patient with right hemianopia **(C)** are shown. Gaze position is depicted in black (fixations shown as circles and saccades as lines). Gray transparent areas are beyond the visual field boundaries. The blue lines represent the courses of the traffic cars and red segments indicate when vehicles are moving on collision course. Speed adjustments of the participant (acceleration or deceleration) result in kinks on the blue lines. The $HVFD_A$ patient shows more gaze shifts, more fixations on cars, larger saccades, larger mean gaze eccentricity, and more speed adjustments (kinks) than the $HVFD_I$ patient, who demonstrates decreased gaze activity. Trial duration is similar between the normal subject and the $HVFD_A$ patient, while the $HVFD_I$ patient completes trials in a shorter period of time. Redrawn from Papageorgiou et al. (2012c).

lead to many cognitive deficits including a decline in memory representation.

Collision avoidance is a cognitively complex task, involving processes such as oculomotor adaptation, speed estimation, scanning and selection of cars with high POC, storage in visual working memory and visuo-motor calibration (Lee, 1976; Simpson et al., 2003). Consequently, together with gaze compensation, the role and function of working memory must be considered when investigating adequate street crossing in hemianopes. Working memory may contribute in three ways (Martin et al., 2007; Machner et al., 2009; Hardiess et al., 2010): (1) supporting visual perception, (2) providing memory-guided saccades, and (3) representing cars and performing calculation of their POC.

Due to the visual field deficit, HFVD patients need to invest additional effort in visual search of the scene in order to select the task-relevant obstacles (cars with high POC), which will be represented in working memory. Insufficient visual exploration or reduced working memory capacity lead to inadequate compensation. A further compensatory option for $HVFD_A$ patients is to use their intact working memory in order to perform memory-guided saccades (Martin et al., 2007; Hardiess et al., 2010; Papageorgiou et al., 2012c), particularly toward the blind hemifield, where no visual input is available. By shifting their gaze to remembered coordinates of the visual scenery in a goal-oriented manner, they are able to save time and avoid unnecessary visual search. In contrast, in $HVFD_I$ patients, working memory capacity seems to be reduced, forcing them to devote a high proportion of their fixations on the intersection in order to create an adequate spatial representation of stationary elements at the cost of moving cars. Consequently, decreased gaze activity and reduced working memory availability result in their inability to solve the task.

SUMMARY AND CONCLUSION

Visually controlled collision detection and avoidance in the traffic intersection task requires contributions from perceptual, visuomotor, and memory components. Studies with normal subjects indicate that gaze movement patterns are task specific in that attention is directed to cars with high POC. Variations of gaze behavior are not predictive of task performance in different subjects or in different trials. It therefore seems likely that the working memory contributions such as judging POC by anticipation of car trajectories, or keeping track of intercepting cars are the major sources of inter-individual variation. This hypothesis is confirmed by the studies with hemianopic patients who can be divided into two groups. In an adequately performing subgroup, memory contribution seems to be intact and visual field loss can be compensated for by additional gaze movements. In an inadequately performing subgroup, such compensation is not possible, presumably due to problems with the required support from spatial memory.

With the data reported here, we expand the models proposed for collision avoidance regarding multiple-object events and gaze movements. For the purpose of selecting relevant objects and estimating their actual POC, bottom-up (pre-attentive) together with top-down (cognitive) processes must be considered. The interaction of both processes implements a representation of objects based on their POC within working memory.

ACKNOWLEDGMENTS

We are grateful to Eleni Papageorgiou and Ulrich Schiefer for the long standing cooperation and helpful discussions. Sabrina Hansmann-Roth was supported by the Deutsche Forschungsgemeinschaft within the Tübingen Centre for Integrative Neuroscience.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 20 February 2013; accepted: 22 May 2013; published online: 06 June 2013.

*Citation: Hardiess G, Hansmann-Roth S and Mallot HA (2013) Gaze movements and spatial working memory in collision avoidance: a traffic intersection task. Front. Behav. Neurosci. **7**:62. doi: 10.3389/fnbeh.2013.00062*

Title:

Allocation of cognitive resources in comparative visual search - individual and task dependent effects

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Abstract:

Behaviours recruit multiple, mutually substitutable types of cognitive resources (e.g., data acquisition and memorization in comparative visual search), and the allocation of resources is performed in a cost-optimizing way. If costs associated with each type of resource are manipulated, e.g., by varying the complexity of the items studied or the visual separation of the arrays to be compared, according adjustments of resource allocation ("trade-offs") have been demonstrated. Using between-subject designs, previous studies showed overall trade-off behaviour but neglected inter-individual variability of trade-off behaviour. Here, we present a simplified paradigm for comparative visual search in which gaze-measurements are replaced by switching of a visual mask covering one stimulus array at a time. This paradigm allows for a full within-subject design. While overall trade-off curves could be reproduced, we found that each subject used a specific trade-off strategy which differ substantially between subjects. Still, task-dependent adjustment of resource allocation can be demonstrated but accounts only for a minor part of the overall trade-off range. In addition, we show that the individual trade-offs were adjusted in an unconscious and rather intuitive way, enabling a robust manifestation of the selected strategy space.

Key index words:

decision making, comparative visual search, working memory, gaze movement, individual trade-off

1. Introduction

A major objective of executive functions [1,2] is the generation of adequate behaviour in order to solve a given task by trading-off the arising costs and benefits in an optimal manner. Costs or pay-offs are consequences in such decision making processes, where the relative values of different behavioural strategies are critical and have to be known or learned.

Cost-benefit analyses are relevant in cognition as well as in economics to promote efficiency. In the field of economics, as example, researchers address the minimum cost flow problem [3]. Here, as part of optimization in a deterministic transportation network, cost flows related to transportation demands (time, energy, etc. of industrial goods) should be minimized leading to economically advantageous solutions. Similarly, cognitive heuristics [4] discusses cost-benefit balancing on cognitive grounds - as a way of increasing efficiency by applying intuitive, rational, and adaptive decisions based on cognitive and perceptual operations (e.g., ACT-R [5]).

In cognitive science, comparative visual search (CVS) is a well established task to investigate decision processes (cost-benefit balancing) under controlled and changing task demands. In CVS subjects have to compare two or more visually separated arrays of items in order to find differences between them [6,7,23,27]. When inspecting one of the arrays, information about the other one has to be kept in mind in order to carry out the comparison. Required memory involvement can be reduced by frequent re-acquisition of information from the reference array. For an optimal overall strategy, the investment in memorization as well as acquisition (exploration) behaviour must be traded-off. Memorization or processing strategies are implemented by visual working memory (WM). Here, the purpose of WM is to enable the short-term retention and manipulation of information in the service of immediate action. Acquisition or sensorial strategies are reflected by gaze movements and involve saccadic (orienting the sensors towards informative areas) as well as fixational (extracting item information) movements.

In general, WM can be defined as a system for maintaining and processing a certain amount of information temporarily for the task at hand [8,9] and is subject to temporal [10-12] as well as storage capacity limitations [13,14]. WM representations decay within several seconds when no active rehearsal processes (refreshing of memory) take place [15]. Regarding storage capacity, visual WM processes information of approximately three to five items at a time coded as integrated object representations, rather than as a collection of separated visual features [14,16]. WM capacity limitations are discussed in two lines of theory. The *fixed-resource theory* [17] conceptualizes WM as limited-capacity channel with a fixed number of slots over which observers can flexibly allocate information with fixed precision. In this view, a complex item (object) will allocate more slots for retention than a simple one. The other class of theories (*flexible-resource*) claims that WM capacity is limited by the availability of processing resources [18]. Here, the maintenance of an item requires some amount of cognitive effort and applying this effort depletes the resource pool. As a consequence, an observer can either maintain a low amount of precisely-represented or a higher amount of less-precisely encoded items before resources run out.

Several studies could show that the investments in acquisition or memorization were balanced so as to optimize the associated time costs [7,19-21], i.e., subjects adjusted the trade-off between acquisition and memorization to minimize overall time when the individual time requirements for the one or other strategy were changed. When overall costs for gaze movements remain low, assumingly the normal state in everyday tasks, subjects will shift the trade-off almost completely to the side of acquisition, i.e., picking up information continuously from the environment just when needed. Such a 'just-in-time' strategy [21] minimizes the investment in memorization and enables WM capacities for other tasks which have to be carried out at the same time. When acquisition becomes more costly (i.e., by increasing the distance between stimulus arrays and so the time needed to capture the information), it was found that subjects increasingly relied on memory processes rather than on gaze movements [7,21,23]. However, the degree of such a shift to memory strategies is restricted by the inherent processing limits of the WM structures involved (see above).

In the present investigation, a simplified desktop version of the CVS paradigm was developed in order to easily manipulate the burden costs and to quantify the strategies for acquisition (gaze shifts between arrays of items) and memorization (fixations needed for information processing within arrays) without measuring gaze behaviour directly.

Acquisition costs can be controlled by varying inter-array separation [7,21-23]. Clearly, spatial separation will always be associated with time needed for re-acquisition [7]. We therefore developed a task in with re-acquisition time is explicitly controlled. During the CVS task one of the two arrays was covered by an opaque mask that could be switched to the other array by hitting a mouse button.

Memorization costs are determined by the required amount of processing, both in perception and memorization. On the perception side, higher costs arise when items entail more features to be extracted, bound, and recognized. Memorization in CVS becomes more costly with respect to information load and the capacity limit of the WM system [13], when items increasingly demand encoding, maintenance, recall, and comparison operations. In our study, we therefore varied the complexity of the comparison items effecting perception as well as memorization in WM [24].

Previous studies on acquisition-memorization trade-offs mostly employed between-subject designs. This leaves open the question whether observed strategy shifts result from subject-specific preferences for one or the other strategy, or from adjustments to the cost constraints applied by all subjects in similar ways. In this study, we use a simplified CVS procedure to assess in one within-subject design both, the strategy distribution in the group and the trade-off behaviour in each subject.

2. Material and methods

(a) Participants, apparatus, and stimuli

Twenty nine volunteers (15 males) aged between 22 and 30 years participated in the study. All subjects were naïve to the purpose of the experiment and had normal or corrected to normal vision. All experiments adhered to the Declaration of Helsinki guidelines and a written informed consent was obtained from each subject prior to participation.

A personal computer (3.1GHz) running MATLAB (MathWorks Ltd) was used for stimulus presentation, experiment control, and recording subjects' responses. The software controlling the experiment incorporated the Psychophysics Toolbox extensions [25]. Stimuli were displayed on a Samsung SyncMaster 931BF monitor (19'', 1280x1024 pixel, 60Hz) driven by the computer's built-in Intel®HD Graphics 2000 graphics board. The viewing distance between subject and monitor was 60 cm (chin rest used) and stimuli were viewed in a dimly lit room.

Each trial (stimulus) of the CVS task consists of two columns (separation: 24 degrees of visual angle) with 24 symbols (randomised order) each. Two types of symbols were used (see figure 1) to manipulate the processing costs: coloured circles as low cost items (i.e., colour condition; red, green, blue, and black; Ø 10 pixel) and silhouettes of animals as high cost items (i.e., object condition; black elk, dog, camel, and cow; all leftward-facing; Ø 30 pixel). For the comparison task, the symbol configurations in the two columns differed at one or two random positions (one- and two-differences, respectively). A maximum number of two differences was introduced to avoid premature trial completion. Because subjects did not know the number of differences, they should not terminate the search after detecting the first difference. During all trials a grey mask was always presented, covering either the left or the right column completely (the right one in the beginning of a trial; figure 1). Between each pair of symbols a black line was always shown (over the mask) guiding the gaze while the mask was presented (see figure 1). During the course of a trial, subjects had to shift the mask between the two columns by clicking one of the two mouse buttons as often as desired. One of three mask delays were used in each trial to manipulate the costs for acquisition, i.e., the onset of mask movement initiated by the mouse click was delayed for 0.0, 0.5, or 1.0 seconds, respectively. Both columns were hidden during the duration of the delay and just the black lines remained. In total, each subject had to process 60 trials in random order (2 symbol conditions x 3 delay conditions x 10 repetitions = 60 trials) by conducting a within-subject design.

-- figure 1 about here --

(b) Procedure

The subjects' task in each experimental condition (trial) was always the same: compare the two columns of items to find the number of differences (one or two) as quickly and reliably as possible. After completion of the comparative search, the key 'spacebar' had to be pressed to finish a trial. Afterwards, the identified number of differences had to be reported verbally. The next trial started automatically after a 3-s fixation phase during which a fixation cross was displayed in the centre of the screen.

Before the experiment started, subjects had to read a written task instruction. Afterwards, three one-difference and three two-difference trials (containing trials of all conditions) were performed to practise the task (particularly the use of the mouse buttons). Subsequent to this practise phase, the experiment started by presenting the first out of 60 trials. At the end of each 20 trials, subjects were allowed to have a break of some minutes. To avoid the uncontrolled influence of verbal rehearsal possibly applied by the subjects to promote memorization of the stimuli, such processes were inhibited by articulatory suppression in all trials. For this purpose, subjects had to repeatedly say out loud three irrelevant syllables (e.g., *'bla-bli-blu'*). In consequence, memory processing was restricted to visual representations in all conditions.

(c) Dependent variables

To investigate the task performance, response time (time for trial completion) as well as error rate (proportion of incorrect trials) were recorded. The two most important measurements (regarding trade-off) were the number of inter-column gaze shifts (i.e. mask switches) and the intra-column processing time. The number of gaze shifts was measured as the number of mouse clicks (to shift the mask) and reflects the acquisition strategy (behaviour) by quantifying the number of gaze shifts between the two columns in each trial. The processing time was measured as the averaged time between two consecutive mouse clicks (minus the delay time) and reflects the memorization strategy (behaviour) by quantifying the averaged time subjects spent within one column before a gaze shift occurred.

(c) Statistical analysis

All ANOVAs reported here were calculated as repeated measurement ones. Effect sizes are reported using partial eta-squared (η_p^2) for all parametric tests. *Post-hoc* analyses were always done with Bonferroni corrected α-values. The results of these *post-hoc* comparisons are denoted within the corresponding figures reflecting conventional significance levels (unmarked: n.s.; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Error bars in all figures indicate standard error of the mean.

3. Results

(a) Task performance: errors and overall response times

Error rate was quantified by the proportion of the wrong number of differences reported by the subjects. Here, the type of difference (one- or two-difference) was not considered. In all conditions subjects showed a high level of performance, i.e., on average between 8 and 9 (out of 10) trials per condition were answered correctly (cf. figure 2). Statistical analysis showed no influence of symbol or delay condition on error rate (Friedman-ANOVA: $chi^2_5 = 9.96$, $p = 0.08$).

-- figure 2 about here --

Response time was analysed by averaging the total time subjects needed to finish a single trial in each condition (figure 2). A two-factorial ANOVA with symbol (colour vs. object) and delay condition (0.0, 0.5, and 1.0 s) as factors was conducted. We found significant main effects of symbol type ($F_{1,28} = 58.76$, $p < 0.001$, $\eta_p^2 = 0.68$) and delay ($F_{2,56} = 4.32$, $p < 0.05$, $\eta_p^2 = 0.13$). No interaction was found ($F_{2,56} = 2.9$, $p = 0.063$, $\eta_p^2 = 0.09$). Compared to coloured symbols, response time for the object stimuli was significantly increased about 10 s in all delay conditions (see figure 2).

(b) Adjustment of acquisition and memorization strategies

To quantity acquisition, the number of (inter-column) gaze shifts was identified. As a measure of memorization, the (intra-column) processing time was calculated. Both measures were analysed for all conditions (see figure 3).

-- figure 3 about here --

Irrespective of symbol type, the number of gaze shifts was reduced when delay increased. In contrast, the processing time was found to increase when delay times were prolonged. This effects were significant in a two-factorial ANOVA for each dependent variable; main effect of delay: on gaze shifts ($F_{2,56} = 5.57$, $p < 0.01$, $\eta_p^2 = 0.17$) and on processing time ($F_{2,56} = 7.83$, $p < 0.01$, $\eta_p^2 = 0.22$). Results of the pairwise comparisons between the three levels of delay are shown in figure 3 for both measures. As well as delay, also the type of symbol was influential concerning gaze shifts and processing time (see figure 3). Compared to the colour condition, both variables showed significantly increased values in the object condition when applying a two-factorial ANOVA; main effect of symbol type: on gaze shifts ($F_{1,28} = 45.21$, $p < 0.001$, $\eta_p^2 = 0.62$) and on processing time ($F_{1,28} = 12.1$, $p < 0.01$, $\eta_p^2 = 0.3$). Significant interactions between delay and symbol type were only identified for processing time ($F_{2,56} = 6.12$, $p < 0.01$, $\eta_p^2 = 0.18$).

Interestingly, a left-right asymmetry was found for processing time (figure 4). Here, subjects spent always more time within the left than the right column when processing the symbols. By conducting pairwise comparisons (paired *t*-tests) this left-right asymmetry effect was found as significant in all conditions (see figure 4).

-- figure 4 about here --

(c) Trade-off between acquisition and memorization strategies

Through conducting a complete within-subject design, trade-off variations (adjustments) provoked by all symbol type and delay conditions could be assessed in each subject. In figure 5*a* the distribution of these individual trade-offs are shown as a bivariate regression between the number of gaze shifts and processing time. Subjects employed markedly different strategies ranging from strong acquisition preference (high n, small T_P) to strong memory preference (small n, high T_P). Data regression was calculated as power function relation with $r = 0.72$. Note that the variance between subjects was much larger than that within subjects (see figure 5*a*). Still, the overall processing time, re-calculated from the regression line as $T_P * n \propto n^{0.15}$ does not seem to depend substantially on strategy. Interestingly, no subjects where identified using small (lower-left region in plot) or large (upper-right region) amounts of both strategies.

-- figure 5 about here --

Condition related trade-offs between number of gaze shifts and processing time are shown in figure 5*b*. Here, the values are calculated by averaging over subjects and are the same as shown separately for each variable in figure 3. The main influence of symbol type on the trade-off became obvious when presenting the data in this bivariate manner (i.e., much more variance between symbol type than between delay). To illustrate the trade-off adjustment (figure 5*b*) on the individual level, the strategy distributions of the ten trials per condition were shown for two representative subjects (figure 5*c* and *d*). Here, the mean values per condition follow the same pattern also visible in figure 5*b*. In addition, the error ellipses also align to the overall trade-off curve in figure 5*a* and *b.*

-- figure 6 about here --

To show the trade-off stability over trials, both main variables where analysed regarding trial order (from 1 to 10). Clearly, trade-off adjustment is independent of trial number as shown exemplarily for gaze shifts in all object conditions (see figure 6). This shows that subjects do not systematically change their strategies during the course of the experiment.

4. Discussion

In the wild, humans and other animals manage to successfully select among many possible courses of action available at every instant. In this article we addressed the task of comparative visual search (CVS) as an example of a cost flow problem which is central to optimal decision making. CVS involves two behaviours, which can relatively easy be controlled, manipulated, and quantified, i.e., information acquisition (manipulated by mask delay; quantified by number of gaze shifts) and memorization (manipulated by symbol complexity; quantified by processing time). It is important to note that both behaviours are common and frequent in daily life, and burden the performing subject with costs to be handled in an optimal manner during the course of decision making [7,20].

Experimental conditions were selected to ensure an overall balanced level of difficulty, i.e., subjects were able to perform all task conditions within a comparable error range between 10 to 25% (see figure 2). Subjects' selection of behavioural strategies resulted in a general increase of the time needed to finish one trial (response time) when search items belonged to the more complex object category (figure 2). Also in this object condition, but not in the colour one, search times increased with delay durations.

In consequence of the costs for memorization and acquisition associated with the experimental conditions, both processing time and number of gaze shifts were adjusted significantly as shown in figure 3. In general, the number of gaze shifts was reduced when costs for acquisition behaviour increased. This effect was much more pronounced in the object condition than for colour (cf. also figure 5*b*). Contrary to the number of gaze shifts, the processing time was increased for longer delays, again with larger effects in the object condition. The general increase of response time in the object condition thus results from a combined increase of both variables.

Furthermore, and in agreement with other studies [20,21] we found a stable strategy selection (see figure 6) already with the first trial in each condition, i.e., no learning of costs and hence no adaptation of strategies occurred during the experiment. We assume that all sub-tasks needed in CVS (eye movements, recognition, encoding, maintenance, etc.) and their respective costs are known in advance from everyday actions, and that all subjects are therefore able to adapt instantly to the various conditions. Interestingly, subjects were not aware that they did adjust their strategies, i.e., if questioned, they reported no explicit or conscious access to their decisions about a certain strategy.

In conclusion, the reported overall findings are in line with existing data on strategy selection published for visual search [7,23,26,27], block-copying [21,22], and a brick-sorting task [20].

In the course of the task, CVS must be segmented into a certain amount of cycles each consisting of four phases: recognition and encoding, inter-column gaze shift, recognition and comparison, and inter-column gaze shift back to the encoding side (see also [6,7]). Since prolonged processing times for the left column were found in each condition (figure

4), we argue that encoding and comparison are generally lateralized with encoding predominantly in the left column and comparison predominantly in the right, a finding also reported in a previous CVS study [7]. This may be related to the standard reading direction in the participants' native language.
For the processing of the objects items (as compared to the colour ones) increased resources are needed for memory encoding and maintenance. In table 1 we show processing time per item, T_I, as a measure of encoding effort, and the number of items processed in each cycle, M_C, as a measure of (inverse) maintenance cost. In the object condition, T_I was doubled while M_C was reduced by 0.5 items, irrespective of delay. We therefore conclude that the higher difficulty level of object items is reflected by an increased effort in both processes, encoding and maintenance.
In our study, the amount of items stored in WM never reached the assumed maximal capacity of four to five [14], not even in conditions with the highest acquisition and the lowest memorization costs. Averaged over subjects, M_C varied between 1.22 (objects condition, delay = 0.0 s) and 1.85 items per cycle (colour condition, delay = 1.0 s). Individual scores were found beyond these limits, but never exceeded 3.2. WM loadings below commonly accepted measures were also found in other tasks [7,20,21]. As explanation, additional demands in attention, executive function, or memory that are not obvious to the experimenter have been discussed [20]. Also, the expected value or execution cost of performing different strategies may influence the preference for the sub-strategies needed in each trial [28,29]. Such values could be influenced by reward, or different task instructions and can change the preferences for perceptual encoding or WM use.
The main motivation for this study was to develop a means to analyse trade-off strategies of individual subjects in order to compare these with the general strategy selection of the population. Figure 5a shows the preferred strategies for each subject in a strategy space spanned by number of gaze shifts n and processing time T_P. Individual strategies follow a power law ranging from strong preference for acquisition (relying on gaze shifts, lower right part of curve) to an equally pronounced preference for memorization (relying on WM, upper left part of curve). Here, the variability between subjects was larger than intra-individual variability. Preferred strategies never fell in the lower-left or upper-right corners of the strategy space. This may reflect the fact that subjects had been instructed to "perform as fast and correctly as possible". The quest for fast performance prevents simultaneous use of high acquisition rate and long processing times (upper right corner) while the need for low error rates prevents subjects from using neither of these strategies (lower right corner). The total investment in terms of time (response time) amounts to T_P times n which would be the same for all subjects if the exponent of the power regression in figure 5a was -1.0. Indeed, we found a rather similar value of -1.15. This is in line with the fact that response times depend only weakly on delay (see figure 2 and above). One possible explanation of this result is that all subjects interpreted the instruction "as fast as

possible" roughly in the same way, allowing about the same amount of working time. This shared sense of a reasonable timing may be triggered by the duration of the experimental delays which rendered timing improvements in the millisecond range meaningless.

On top of the strategic preferences identified for each subject, we found condition dependent adaptations of strategy that follow the same trade-off pattern, albeit at a somewhat smaller scale. Figure 5b shows the strategies for each condition, averaged over all subjects. Between the symbol conditions (colour, object) an overall increase in effort is clearly visible. Within the symbol conditions, the number of gaze shifts correlates negatively with delay duration. Note that this negative correlation is also visible in the error ellipses of figure 5c and d showing the results for two individual subjects. The task-specific pattern centred at each subjects' overall strategy is clearly visible.

Taken together, these results clearly show that population-based trade-off-curves are a result of two factors, inter-subject variation of preferred strategies, and within-subject adjustment of resource allocation. For the variation between subjects, individual weightings of the respective costs may play a role. Indeed, such differences are found frequently and attributed to a varying efficiency in the encoding and maintaining of information [30] or in associated executive functions [31]. In future work, intra-individual measures of WM (e.g., attentional span, complex span, executive processing, etc.) need to be recorded in parallel to decision making and minimum cost flow tasks in order to understand the memory processes underlying optimal decision making.

Acknowledgements

We would like to thank A. Sarikaya and N. D. Martin for their help in running the experiments.

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Table and figure captions

Table 1. Amount of items maintained per cycle (M_C) and encoding time per item (T_I) in seconds) given for each mask delay (d = 0.0, 0.5, and 1,0 s) and for colour (c) and object (o) items. M_C equals the total amount of items divided by number of gaze shifts (n). T_I equals the processing time (T_P) divided by M_C.

	$d_{0.0}$		$d_{0.5}$		$d_{1.0}$	
	c	**o**	**c**	**o**	**c**	**o**
M_C	1.74	1.22	1.84	1.32	1.85	1.38
T_I	0.69	1.23	0.66	1.23	0.69	1.32

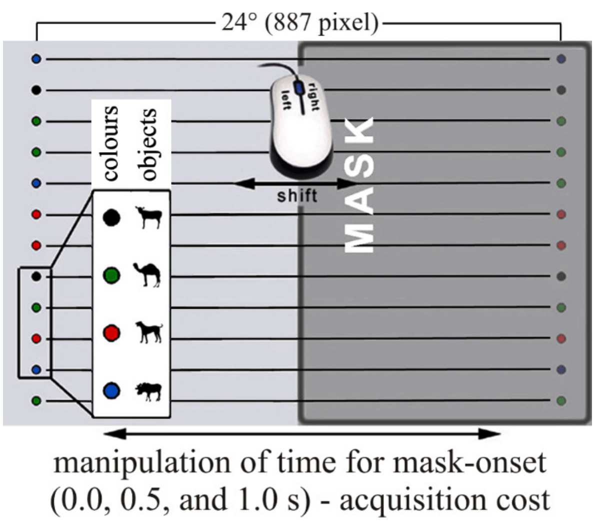

Figure 1. Task setup. A stimulus image consists of two columns (column distance: 24°) with 24 items each (only 12 shown in the figure). Items were either coloured circles (blue, red, green, and black; see inset) or black silhouettes of animals (elk, dog, camel, and cow; see inset). A grey mask (shown here as transparent for sake of illustration) was always covering one column and could be shifted (to the other column) by clicking one of the two mouse buttons. The time for mask-onset after each click was manipulated by using one of the three mask delays. During the time of delay both columns of items were hidden and only the black lines were presented. (Online version in colour.)

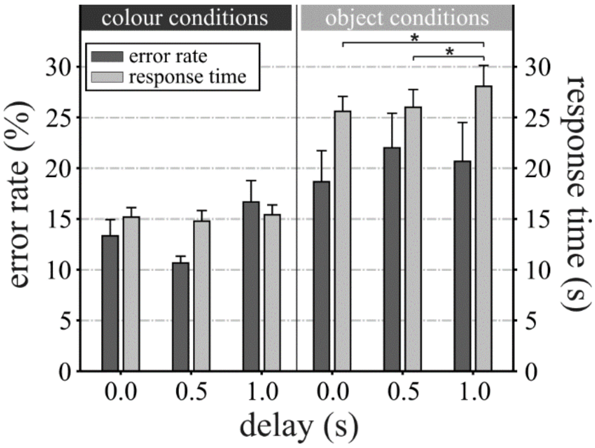

Figure 2. Task performance. Error rate (dark grey) and overall response time (grey) averaged over subjects are shown for all experimental conditions (left: colour and delay; right: object and delay).

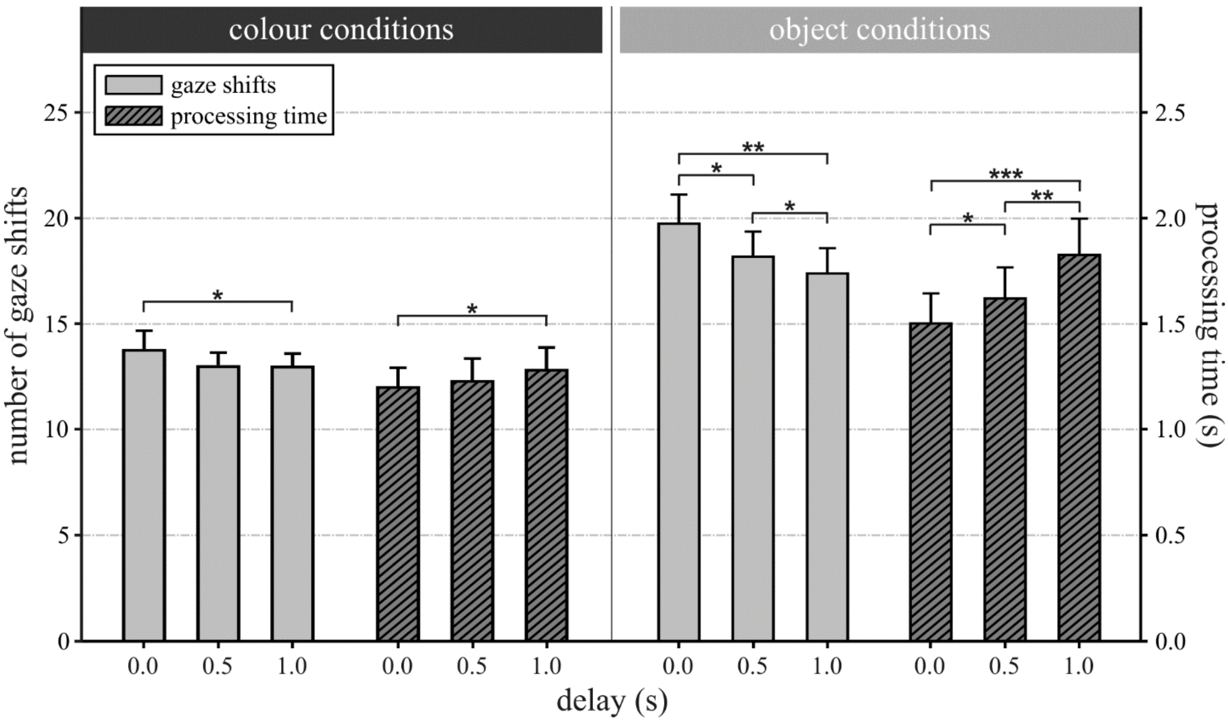

Figure 3. Adjustment of acquisition and memorization strategies (behaviour). Number of (inter-column) gaze shifts as quantity for acquisition (grey bars) and (intra-column) processing time as quantity for memorization (dark grey/striped bars) averaged over subjects are shown for all experimental conditions (left: colour and delay; right: object and delay).

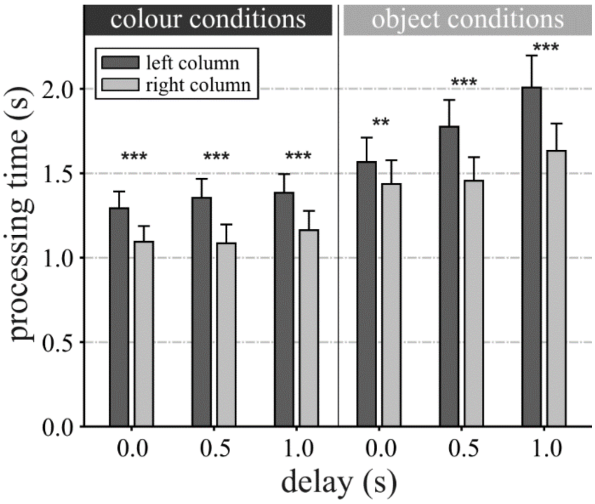

Figure 4. Left-right asymmetry. Processing time averaged over subjects is shown separately for the left (dark grey) and the right column (grey) for all experimental conditions (left: colour and delay; right: object and delay).

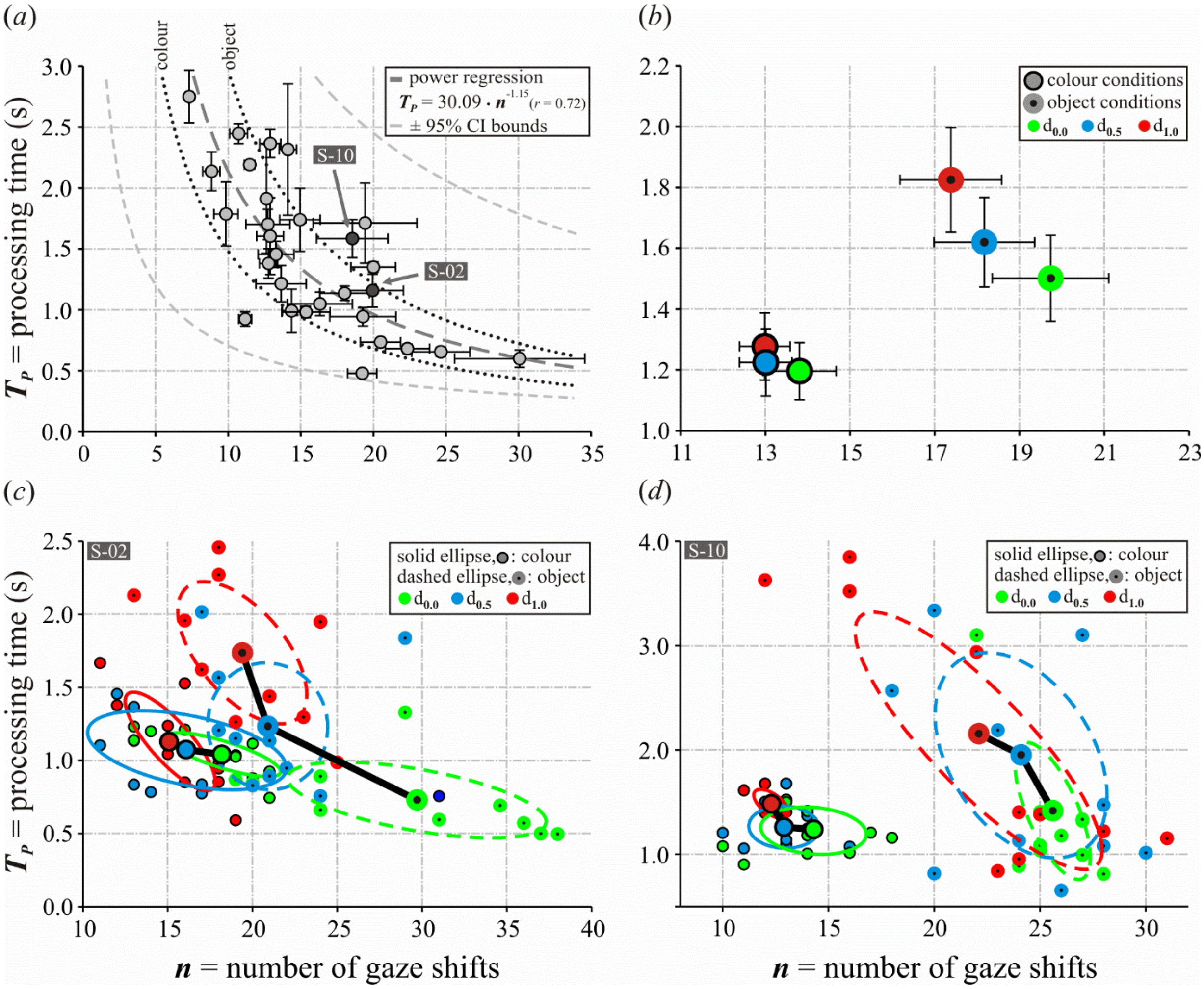

Figure 5. Trade-off between acquisition (n = number of inter-column gaze shifts) and memorization (T_P = intra-column processing time) strategies. Please note the different scaling of the axes between the plots. (*a*) Individual strategies averaged over all conditions are shown for each subject (grey circles with error bars). Regression of the individual strategies (dark grey, dashed line) indicates a power function relation with $r = 0.72$. The ±95% confidence bounds are depicted as grey, dashed lines. In addition, regression lines (power function relations) are plotted (black dotted lines) for colour ($r = 0.64$) and object ($r = 0.76$) conditions separately. (*b*) Delay dependent trade-offs averaged over subjects are shown for the colour (circles with black margins) and the object (circles filled in black) conditions. (*c*) Single trial data (ten trials per condition) with error ellipse and mean value are shown for each condition for subject S-02; marked in (*a*). Means are connected by black lines for all delays in the colour and all delays in the object condition. (*d*) Single trial data (ten trials per condition) with error ellipse and mean value are shown for each condition for subject S-10; marked in (*a*). Means are connected by black lines for all delays in the colour and all delays in the object condition. (Online version in colour.)

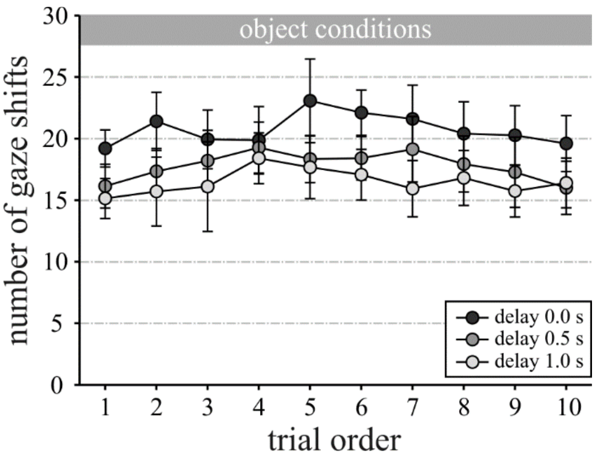

Figure 6. Trade-off stability over trials. Number of (inter-column) gaze shifts (averaged over subjects) is plotted against the trial order for each object/delay condition. Note, in consequence of the experimental design, between the trials of a particular condition there was a variable number of trials from the remaining five conditions.

Strabismus, 18(3), 78–82, 2010

ISSN: 0927-3972 print/ 1744-5132 online
DOI: 10.3109/09273972.2010.502958

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PROCEEDINGS ARTICLE

Task-Dependent Representation of Moving Objects Within Working Memory in Obstacle Avoidance

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ABSTRACT

Purpose: The purpose of the study was the quantitative analysis of the working memory representation of dynamic objects related to gaze movement behavior.

Methods: Eighteen subjects participated in a virtual street-crossing paradigm. The primary task was collisions avoidance. To investigate the representation format, during a sub-task subjects were asked to reconstruct the traffic scene from memory.

Results: The distribution of cars positioned during the sub-task reveals a task-dependent (i.e., collision-relevant) representation of about four cars. In contrast, analysis of gaze behavior did not show a preference for collision-prone cars.

Conclusion: Subjects avoided collisions efficiently by applying a gaze strategy adequate to create a representation that fulfills the demands of the task. Collision-prone cars are more likely to be represented in memory, but not more likely to be fixated.

KEYWORDS: dynamic objects; representation; visuospatial working memory; gaze movements

INTRODUCTION

The prominent role of human vision for the purpose of orienting and navigating successfully is beyond question. But which pieces of information should be selected as important in the complex, everyday surroundings with an almost unlimited amount of visual cues, where all of these stimuli compete for visual attention? Clearly, our brain had to develop selection strategies. Besides task demands that lead to top-down selection processes, two constraints of the human visual system determine the exploration strategies: (i) the retina is limited in resolution and (ii) cognitive processing within the visuospatial working memory (VSWM) (Baddeley, 1986; Baddeley & Hitch, 1974) is limited in capacity (Alvarez & Cavanagh, 2004; Luck & Vogel, 1997). In adaptation to the resolution constraint of the sensors, visual exploration makes use of eye movements. Additionally, the process of visual selection draws attention to stimuli that are relevant for the purpose of the task (e.g., Land et al., 1999; Pelz & Canosa, 2001). This selection process helps to create representations purposefully and to fill the VSWM optimally.

A very important but poorly understood function of vision is the exploration and representation of dynamic visual scenes. Most behaviors and situations involve task-relevant objects that change their positions over time. One example of such a situation is collision avoidance during the crossing of an interception (Geruschat et al., 2003; Whitebread & Neilson, 2000). Although a certain amount of dynamic objects have to be perceived and processed in order to adjust a convenient passing distance, we perform this complex task often without any effort. Until recently, very little was known about the creation of VSWM representations during such dynamic tasks (Fehd & Seiffert, 2008; Narasimhan et al., 2009).

Received 14 May 2010; Accepted 19 May 2010

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The purpose of the present study was to investigate the representation of dynamic objects (i.e., cars) in VSWM using a virtual intersection paradigm with the task of collision avoidance. The content of representation was assessed together with the gaze movements carried out to collect relevant information.

MATERIALS AND METHODS

Subjects

Eighteen normally sighted subjects participated in this experiment. All subjects were students recruited from the faculty of biology in Tübingen. Informed consent was obtained from each subject after the nature and possible consequences of the study were described. The research followed the tenets of the Declaration of Helsinki and was approved by the institutional human experimentation committee.

Equipment

Eye movements were recorded with a head-mounted eye tracker (model 501, Applied Science Laboratories, Bedford, United States). To record head movements, the ART-track/DTrack system (A.R.T. GmbH, Weilheim, Germany) was used. This device tracks a rigid body fixed to the eye tracker (Figure 1, inset picture). Both trackers had a temporal resolution of 60 Hz. Consequently, gaze was calculated by adding the components for eye-in-head and head-in-space movements together.

The experiment was performed using a virtual reality environment displayed on a large, conic projection screen shown in Figure 1. This screen provided a field of view of 150 × 70 degrees to the subject. Subjects were seated upright with their back tightly at the chair and with their head in the axis of the conical screen (eye level at 1.2 m with 1.62 m screen distance). Experimental procedures and rendering of the virtual environment were programmed in the SGI OpenGL Performer™.

Task Design

The primary setup of the task was that of approaching to an intersection and crossing that intersection without having a crash. The intersection road contained two lanes, one for white cars coming from left, and one for red cars coming from the right. Cars were modeled in three lengths (i.e., 5, 7.5, and 10 m; Figure 2). They all drove with a constant speed of 50 km/h. To create realistic traffic situations, we generated exponentially distributed random variables by using the logarithm method (see Knuth, 1997) for calculating the distances between cars. Parameters were adjusted in order to generate a mean traffic density that caused a crash rate of 60% when subjects would cross the intersection with random speed.

Each trial consisted of two phases, the phase of passive approach and the interaction phase.

Phase 1—Passive Approach

During this initial phase, subjects were driven passively with a constant speed of 30 km/h towards the intersection from point S to point E1 (i.e., 31 m, Figure 2). The task for the subjects was to explore the environment, especially the intersecting traffic, in preparation for the active collision avoidance during the second phase. After 3.7 seconds this approach phase was terminated by the appearance of a black bar occluding the entire intersection road with all the cars for 333 ms.

Phase 2—Car Positioning or Collision Avoidance

In half of the trials subjects had to avoid collisions actively after the disappearance of the black bar by adjusting their own driving speed within the range of 15 to 50 km/h from point E1 to E2 (Figure 2). They could accelerate and decelerate smoothly by pushing a joystick forward and backward, respectively. After point E2 (indicated by a white line, cp. Figure 2) subjects were driven passively across the intersection and the experimental program checked for a possible crash. During this last passive stage visual feedback was prevented by hiding the scene. In each of the collision avoidance trials the traffic constellation was generated in a way that subjects would have a crash in case they didn't change their initial speed (i.e., 30 km/h).

In the other half of trials, subjects had to reproduce as precisely as possible the entire traffic situation (i.e., type, direction, and position of cars) as seen immediately before the black bar appeared. For this purpose they saw the empty intersection road from the point E1. Above the road two pools of cars were presented (Figure 3) for the purpose of selection and positioning with the help of the joystick. Subjects had 30 seconds for this reproduction process; remaining time was indicated by a time bar (cp. Figure 3).

Procedure

After instruction of the subject and execution of some test trials (introduced to make subjects familiar with the use of joystick and the task) the tracking devices were calibrated. Additionally, each experimental trial started with a 5-second fixation phase during which a fixation cross was displayed at eye level in the center

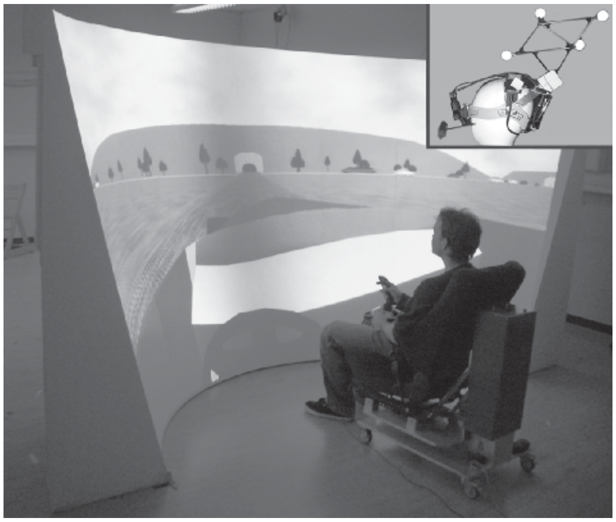

FIGURE 1 Screenshot of the projection screen with the intersection task. Inset picture: picture of the eye tracker with the fixed target for head tracking.

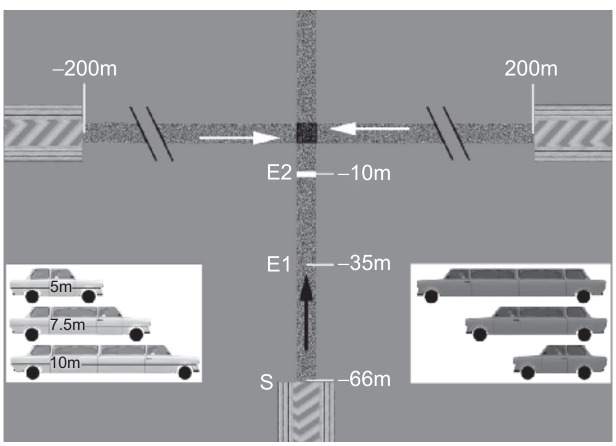

FIGURE 2 Task overview. The black arrow symbolizes the approach direction towards the intersection (dark square) of the subject and the white ones these of the white (from left to right) and red (from right to left) cars. S: starting point, E1: end point of the approaching phase and start point of the interaction phase, E2: end point of the collision avoidance phase.

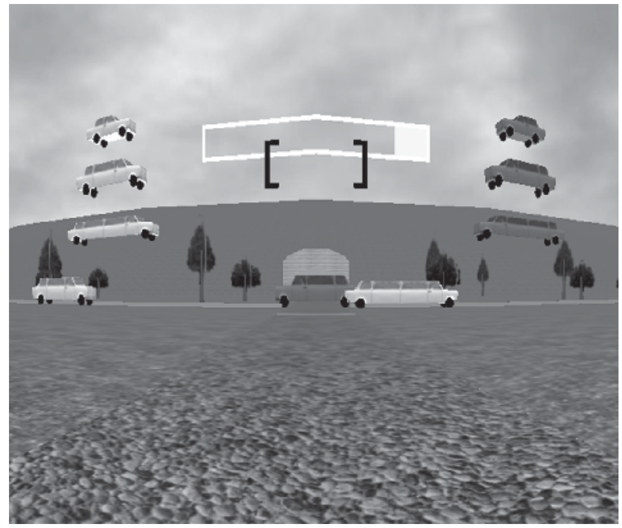

FIGURE 3 Screenshot from the positioning task. Above the intersection road cars out of two pools (i.e., all sizes for each color of cars) could be selected with the black bracket for positioning. The white rectangle shows the remaining time.

of the screen. The total experiment contained 40 trials. Each trial started with the phase of passive approach to the intersection. Subsequently, subjects had to perform either the car positioning or the collision avoidance subtask. Each of these subtasks was presented 20 times in random order.

RESULTS

The primary objective for the subjects was collision avoidance. Subjects showed an overall crash rate of 45.79% ± 13.87%. This crash rate was significantly lower than the 60% chance level for having a crash when crossing the intersection without inspection ($t[18] = 4.47$, $p < 0.001$).

In the car positioning subjects positioned on average 4.12 ± 1.33 cars in each trial while on average 15.55 ± 2.46 cars had been presented in each trial. Figure 4A shows the distribution of cars positioned in each interval. The distribution of red cars (i.e., moving from right to left) reaches its maximum of over 20% for the interval 20 ± 5 m, clearly before the intersection, related to the driving direction of these cars. The same distribution was found for the white cars. Here, the maximum of positioned cars was within the interval −10 and −20 ± 5 m, and thus clearly before the intersection, too. Additionally, there was a significant difference between the number of positioned cars driving towards the intersection and cars leaving the intersection ($t[36] = 16.4$, $p < 0.001$).

In comparison with the positioning distribution the distribution of gazes on cars related to the position of the cars at point E1 was calculated for each interval (Figure 4B). Both distributions for gazes on red and on white cars are almost evenly distributed over the complete range of intersection but show an accumulation of gaze events for the range ± 40 m. No separation of the two distributions due to driving direction was observed. Furthermore, out of all gazes, just 49% were directed towards cars. In Figure 5 a representative gaze trajectory during the approach phase is illustrated.

DISCUSSION

The investigation of gaze behavior in and VSWM representation in a collision avoidance task with moving

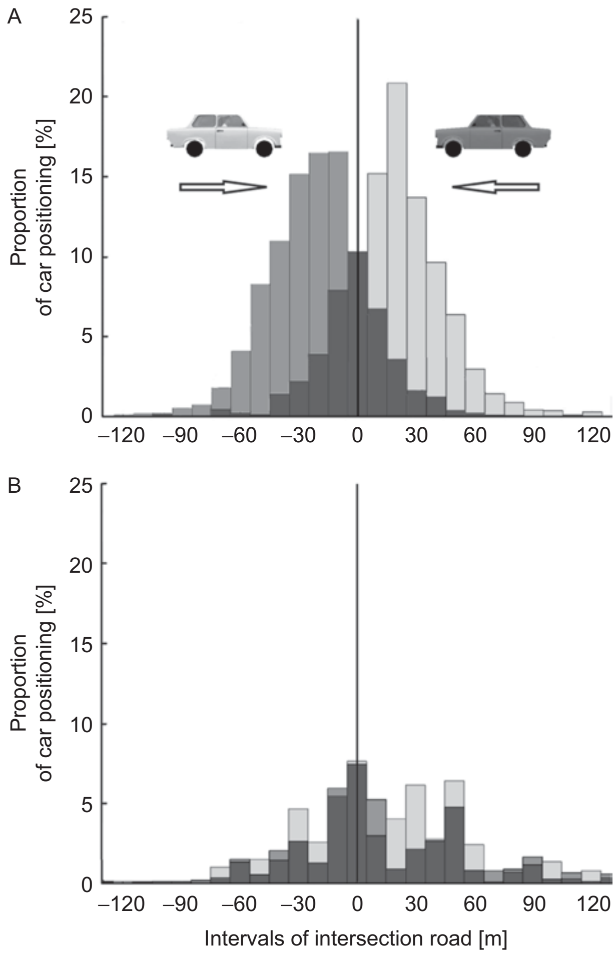

FIGURE 4 Distribution of gaze and car positioning events plotted for the range of the intersection road visible for subjects at point E1 (see Figure 2). (A) Proportion of cars positioned within each 10-m interval averaged over subjects for white cars moving from left to right (gray bars) and for red cars moving from right to left (light gray bars). Dark gray bars symbolize the overlap of the two distributions. (B) Proportion of gazes on cars within each 10-m interval averaged over subjects for white cars moving from left to right (gray bars) and for red cars moving from right to left (light gray bars). Dark gray bars symbolize the overlap of the two distributions. Gazes to one car are shown at the position that the car assumed when the observer was at E1.

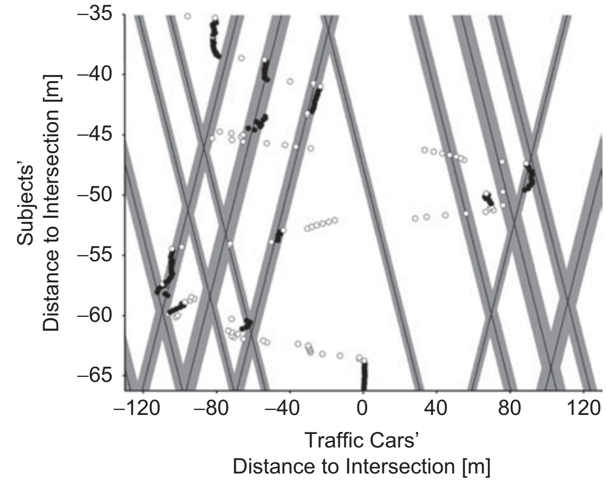

FIGURE 5 Gaze trajectory example for a single approach phase. Gray lines symbolize the positions of traffic cars visible at each particular position of the subject (i.e., distance to the intersection). Widths of oblique lines indicate the length of cars. Black circles show fixational and white circles saccadic episodes of the gaze trajectory.

objects was the purpose of the study. As the main result we identified a task-related representation of the moving obstacles (cars). Positioning performance reveals a representation format highly dependent on the task relevance of cars, that is, their probability to collide with the subject. More precisely, distant cars and those leaving the intersection were represented very rarely whereas cars with driving direction towards the intersection and within the time window of subjects' intersection approach were represented preferentially. When the observer is at E1, cars that actually would hit the observer when crossing the street will be located at positions of 53.75 ± 1.25 m from the intersection point. Since most cars were placed at about ± 20 m, task relevance of representation seems to be compromised by a general, straight-ahead strategy or by the phenomenon of representational momentum (Freyd & Finke, 1984). Furthermore, subjects positioned during one trial just a limited amount of cars, that is, in the range of four. This finding is in concordance with previous results concerning VSWM capacity (Intriligator & Cavanagh, 2001; Pylyshyn & Storm, 1988; Yantis, 1992). The restricted capability could be based on processing limitations of the memory (Cowan, 2001; Miller, 1956). Alternatively, limitations could be based on the restriction of a conscious access onto memory contents. This possibility occurs with our task design where subjects had to position the cars actively out of memory. However, our results allow no distinction between these two alternatives.

Besides positioning, the gaze movement patterns were analyzed while subjects approached the intersection passively. In contrast to the distribution of cars positioned, the distribution of gazes on cars did not reflect the collision relevance of cars. Here, gazes are rather evenly distributed over the intersection road. In order to fill the VSWM and build up a representation, subjects fixated on an average of four cars. However, these fixated cars are not necessarily the positioned ones as indicated by the two different distributions. The results indicate that target selection (by gaze movements) is less task-specific than target representation (in VSWM). Attentional processing in dynamic obstacle avoidance thus seems to be an interaction of bottom-up (mostly forward gaze) and top-down (look for collision-prone cars) processes. Future work is needed to shed more light on the process of visual exploration regarding a collision avoidance paradigm. As useful and well-elaborated approach to studying allocation of resources regarding attention and VSWM under dynamic conditions multiple object tracking (Pylyshyn & Storm, 1988) could be applied. With this, task factors that play a role in the ability to track objects such as grouping of the moving items (Yantis, 1992), the spacing between items (Alvarez & Franconeri, 2007; Intriligator & Cavanagh, 2001), the relative position of items in the visual field (Alvarez & Cavanagh, 2005; Carlson et al., 2007), or the cohesiveness of the moving items (van Marle & Scholl, 2003) were identified.

ACKNOWLEDGMENT

***Declaration of Interest*:** The authors report no conflict of interest.

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Vision Research 50 (2010) 1158–1172

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Functional compensation of visual field deficits in hemianopic patients under the influence of different task demands

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ARTICLE INFO

Article history:
Received 21 April 2009
Received in revised form 29 January 2010

Keywords:
Homonymous hemianopia
Functional compensation
Comparative visual search
Visual sampling
Eye movements
Head movements

ABSTRACT

We investigated the task-specific role of eye and head movements as a compensatory strategy in patients with homonymous visual field deficits (HVFDs) and in age-matched normal controls. All participants were tested in two tasks, i.e. a dot counting (DC) task requiring mostly simple visual scanning and a cognitively more demanding comparative visual search (CVS) task. The CVS task involved recognition and memory of geometrical objects and their configuration in two test fields. Based on task performance, patients were assigned to one of two groups, "adequate" ($HVFD_A$) and "inadequate" ($HVFD_I$); the group definitions based on either task turned out to be identical. With respect to the gaze related parameters in the DC task we obtained results in agreement with previous studies: the gaze pattern of $HVFD_A$ patients and normal controls did not differ significantly, while $HVFD_I$ patients showed increased gaze movement activity. In contrast, for the more complex CVS task we identified a deviating pattern of compensatory strategy use. Adequately performing subjects, who had used the same gaze strategies as normals in the DC task, now changed to increased gaze movement activity that allowed coping with the increasing task demands. Inadequately performing patients switched to a novel pattern of compensatory behavior in the CVS task. Different compensatory strategies are discussed with respect to the task-specific demands (in particular working memory involvement), the specific behavioral deficits of the patients, and the corresponding brain lesions.

1. Introduction

Movements of eye and head (i.e. gaze), together with attentional shifts are a key element of visual behavior in complex environments. Patterns of gaze shifts will depend on a number of factors, including the size and layout of the visual field, central visual processing capacities, short-term and long-term memory, and specific task demands. Generally, the efficiency of gaze movement strategies is determined by the acquired perceptual database (see Boothe, 2002) and the adequacy of this database for the current task. Studies with patients suffering from visual field deficits are instrumental in assessing the gaze strategies and their adaptation to reduced information intake and maybe reduced processing capacities. As compared to healthy subjects, patients' strategies may differ with respect to scanpath pattern and memory involvement, leading to various levels of functional compensation. In this study, we investigated the functional compensation achieved by homonymous hemianopes and the dependence of the used gaze strategies on tasks constraints and visual field limitations.

Patients with homonymous visual field defects (HVFDs) are impaired by a restricted visual field due to scotomas caused by unilateral post-chiasmal brain damage (Zihl, 1994). Common causes are cerebrovascular accident, traumatic brain injury, and tumors (e.g. Kerkhoff, 1999; Zihl, 2000). The visual system of these patients lacks up to one hemifield (in case of complete homonymous hemianopia). Consequently, these patients have difficulties in reading (e.g. McDonald, Spitsyna, Shillcock, Wise, & Leff, 2006; Zihl, 1995a), may collide with obstacles on the affected side (Zihl, 2000), and generally have problems to comprehend entire visual scenes at a glance.

However, some hemianopic patients are able to compensate for the visual limitation, at least to a certain extent, by performing additional, adaptive eye and head movements leading to an efficient use of the remaining visual field. Ishiai, Furukawa, and Tsukagoshi (1987) describe one obvious adaptation used by hemianopic patients. When viewing simple pattern, normal controls focus mainly to the centre of a display while hemianopic patients concentrate on the side of their visual field defect. The shift of the fixation point towards the hemianopic side brings more of the visual scene into the seeing hemifield (Gassel & Williams, 1963).

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doi:10.1016/j.visres.2010.04.004

Furthermore, Meienberg, Zangemeister, Rosenberg, Hoyt, and Stark (1981) identified different compensatory strategies in HVFD patients when faced with simple visual targets which were presented in a predictable or unpredictable fashion. In more detail, compensatory effects identified in many studies showed that patients spend more (search) time in the stimulus half corresponding to their visual loss, perform generally more saccades but with decreased amplitudes when directed into the area of the visual loss, and differed therefore in their scanpath pattern as compared to healthy subjects (e.g. Kerkhoff, 1999; Pambakian et al., 2000; Tant, Cornelissen, Kooijman, & Brouwer, 2002; Zangemeister, Meienberg, Stark, & Hoyt, 1982; Zangemeister & Oechsner, 1996; Zihl, 1995b, 1999, 2000). Also in visual search tasks, hemianopes exhibited longer total search times, shorter and more frequent fixations, and shorter saccades than healthy subjects (Chedru, Leblanc, & Lhermitte, 1973; Machner et al., 2009). Overall, the HVFD patients' bias toward the blind hemifield has been suggested to be a compensatory strategy that aims to partially overcome the loss of input from the affected side (Zihl, 1995b).

With the introduction of a visual sampling task (i.e. the dot counting paradigm, see below), Zihl (1995b) was able to subdivide the investigated collective of patients into two groups, depending on whether their search time exceeded the highest value found in the group of normal subjects (these patients were denoted as "pathologic hemianopics") or not (this group was denoted as "normal hemianopics"). Interestingly, for the "normal hemianopics" the author identified effective search patterns comparable to healthy subjects. In contrast, the scanpaths of the "pathologic" group were significantly longer and showed a higher number of fixations not only in the affected but also in the "intact" hemifields. Furthermore, it was concluded (Zihl, 1999, 2000) that the presence, time since, and severity of the HVFDs could not sufficiently explain the observed scanning deficit, and that additional factors are crucial for explaining the impaired oculomotor scanning. In general, it seems that patients with the same amount of visual field loss, as assessed by perimetry, show different degrees in their functional compensation and behavioral performance.

In the majority of studies concerning the oculomotor compensatory behavior, the stimuli were presented on computer screens and were therefore limited in field of view. The most prominent paradigm used to objectively and quantitatively assess oculomotor compensational behavior is the dot counting task introduced by Zihl (1995b, 1999, 2000). This counting task assesses the process of visual scanning without the primary involvement of more complex visual functions (Zihl, 1999).

Little is known about the visual exploration strategies applied by individual patients when dealing with different and cognitively more demanding tasks. Such studies are needed to understand the way how the visual system chooses among different compensation strategies and to better evaluate the performance of hemianopic patients. Therefore, the main focus of the present study was to investigate the task performance and the gaze related strategies of patients with long lasting homonymous hemianopia in two visual experiments differing in their demands concerning visual processing. We established an innovative experimental setup with a large projection display (i.e. full field of view) and simultaneous measurements of eye and head movements. In the first experiment, we used a dot counting task with an enlarged stimulus size as compared to the original setup (cf. Zihl, 1995b). The aim of this experiment was to validate the new setup with a standard paradigm and to extend previous results including the oculomotor compensation strategies (Zihl, 1995b, 1999) to larger fields of view. The second experiment used a comparative visual search task (Hardiess, Gillner, & Mallot, 2008; Pomplun et al., 2001) as a more cognitively challenging paradigm. In this paradigm two almost identical stimulus hemifields (i.e. cupboards filled with geometrical objects) have to be explored in order to find the number of differences between them. For both experiments, two patient groups were defined according to task performance. While previous group classifications were based on comparisons of the performance of patients with healthy controls (Zihl, 1995b) or on patients' behavior in everyday life (Zihl, 1999), we developed a procedure based only on intrinsic task performance (i.e. error rate and response time) in each experiment. For the resulting patient groups, task performance together with the applied gaze strategies was analyzed and compared to the results from healthy controls in order to identify functional compensation patterns employed by the HVFD patients. We will point out that patients of both groups show different degrees and strategies of visual compensation in the different tasks. These differences are discussed in terms of brain lesions and cognitive task demands.

2. Methods

2.1. Experimental setup

To enable standardized and completely programmable experimental environments, all experiments were performed applying virtual reality (VR) technology programmed in C++ using OpenGL® libraries. The computed VR stimuli were presented on a large, curved projection screen as shown in Fig. 1. The geometrical shape of the projection screen was that of a conic shell with a vertical axis, an upper radius of 1.83 m, and a lower one of 1.29 m. Subjects were seated upright with their back tightly at the chair and with their head in the axis of the conical screen (eye level was adjusted at 1.2 m with 1.62 m screen distance). The screen provided a horizontal field of view of 150° and a vertical one of 70° (45° downwards plus 25° upwards). To illuminate the whole projection screen, two video projectors each with 1024 by 768 pixel resolution and a fixed 60 Hz frame rate were used. The light in the experimental lab was dimmed nearly to complete darkness to avoid disturbing cues from the surround.

The projection setup was running on a 2.6 GHz PC under Linux RedHat 9.0 as operating system (graphic card: NVIDIA® Quadro4® 980XGL with dual video projector connection). The spatial resolution of the generated images was 2048 by 768 pixels. The SGI® OpenGL Performer™ was used to render the virtual environments as well as to handle the programs for the experimental tasks.

Fig. 1. Image of the curved projection screen and the displayed comparative visual search paradigm (cupboard task). Subjects sit comfortably in a high adjustable seat while performing the experiments. Small picture: ASL501 eye tracker with fixed rigid body enabling head tracking.

Eye-in-head movement recordings were realized with an infrared light based, head mounted and lightweight eye tracker (bright pupil type, model 501 from Applied Science Laboratories, Bedford, USA). The tracker uses the pupil-corneal-reflection method and enables an accuracy two degrees or better, depending on the eccentricity of the eye position. Real time delay was 50 ms. To record head-in-space movements, an infrared light based tracker system (ARTtrack/DTrack from ART GmbH, Weilheim, Germany) with 6 degrees of freedom, 0.1° accuracy, and a real time delay of 40 ms was used. A configuration of four light reflecting balls fixed to the eye tracker device and thus to the head (see Fig. 1) provided the tracking target for the head tracking system. Both trackers had a fixed temporal sampling frequency of 60 Hz. The online position recordings from eyes and head were transmitted via socket connection to an experimental PC for storage.

2.2. Experimental tasks

2.2.1. Dot counting

Visual sampling was assessed using the dot counting (DC) task introduced by Zihl (1995b). This task probes pure visual sampling without any further (top-down) identification of the stimulus material (Zihl, 1999), or the primary involvement of other complex high-order visual functions (Tant et al., 2002). The memory demands during the DC task are small and restricted to spatial memory of the scanpath.

To perform the DC task in the present study, subjects had to scan consecutively three different dot patterns. Each pattern included 20 bright dots scattered randomly over the projection screen. The background color was dark grey. The dots were presented within a field of 60° horizontally by 40° vertically; this differs from the original study (Zihl, 1995b, 1999) where 40° by 32° were used. All dots were arranged with a minimal spatial separation of 7° and the diameter of a single dot was 54 min of arc. For reasons of comparability with Zihl's work, only eye movements were allowed and recorded whereas head movements were restricted by using a chin rest.

Subjects were instructed to scan the pattern and to count dots in silence as quickly and reliably as possible and to terminate each trial by pressing a button on a joystick. Afterwards they were asked to report verbally the number of dots. No instruction was given how to proceed during scanning. Each trial started with the fixation phase to the fixation cross (see below) after pressing the joystick button.

2.2.2. Comparative visual search

Comparative visual search (CVS) requires observers to sample, identify, store, and compare corresponding portions of two display halves, which involves processes such as visual search, eye movements, and visual working memory (Gottlob, 2006). CVS differs from (non-comparative) visual search in the way in which distracters are defined: In (non-comparative) visual search, targets are distinguished from distracters by some physical (bottom-up) feature dimensions which may be pre-attentively apparent as in feature search, or may require a minimal set of computations as in conjunction search (Wolfe, 1994). In contrast, CVS target pairs can be identified only by comparison of the display halves, requiring memory and gaze shifts. Targets are defined by a lack of correspondence across the two halves of the display. Thus, this task addresses a number of components tested neither by the DC task nor by standard visual search, including: (i) storage of a collection of objects or features in visual working memory, (ii) gaze movements to acquire "snapshots" for the purposes of comparison, and (iii) a "comparator mechanism" to signal when corresponding items differ in shape and/or color. In conclusion, we argue that CVS involves visual working memory much more than visual search or counting of dots.

In the present CVS paradigm (cf. Hardiess et al., 2008; Pomplun et al., 2001), two cupboards equally filled with simple objects in four geometrical shapes (triangles, circles, diamonds, and squares) and four different colors (green, blue, yellow, and black) were used as stimuli (see Fig. 2). Each cupboard included 20 objects in four shelves. Each shelf included five objects in a row and one cupboard subtended 30° of the subjects' horizontal field of view. The diameter of each object was 3°, the horizontal separation between two objects was 5°, and the vertical separation between shelves was 11°. The horizontal separation between the centers of both cupboards was 60° (±30 distance from the subject's straight ahead direction).

The object configuration in the two cupboards was either completely equal (zero target condition) or differed at one or two positions (one and two target conditions, respectively). Target objects differed in shape only whereas all other object pairs had identical features (functioning as distracters). A maximum number of two targets were introduced, to avoid premature trial completion. Since subjects did not know the number of targets, they could not terminate the comparative search after detecting the first target. A complete cupboard task session consisted of 21 trials presented in random order (three target conditions × seven repetitions). The object configuration regarding targets and distracters was randomized for each trial. Contrary to the DC task, subjects were free to move their head together with eyes to find the number of targets (i.e. zero, one, or two) as quickly and reliably as possible. No instruction was given how to proceed with searching. Subjects had to terminate each trial by pressing a joystick button and reported the number of targets verbally. Each trial started with a fixation phase to the fixation cross (see below) after pressing the button. Participants were free to take breaks in between trials if desired.

2.3. Procedure

Subjects were seated in the chair and the eye tracker was calibrated by displaying a 9-point calibration pattern on the projection screen. For the procedure, head movements were prevented with a chin rest. The target for head movement tracking was calibrated also with fixed head. After completion of the calibration procedure, subjects started to perform the DC paradigm. During the task the head remained on the chin rest to avoid head movements. Immediately after finishing the first experiment, subjects had to proceed with the CVS experiment. For that task the head was set free and unrestricted head movements became also possible.

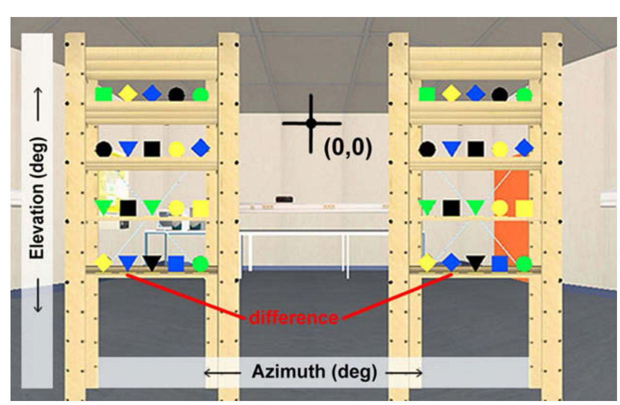


Fig. 2. Screenshot of the cupboard experiment as used in the comparative visual search task. In this example trial a one target condition is shown. Gaze position is expressed in angles (azimuth, α and elevation, β) with respect to the point of origin.

In both paradigms, each single experimental trial started with a five second fixation phase during which a fixation cross was displayed at eye level (1.2 m elevation) in the center of the projection screen (point of origin, cf. Fig. 2). During this phase participants had to rotate the head to align the naso-occipital axis with the fixation cross (automatically assured by chin rest in DC task), followed by fixating the cross with the eyes. All gaze (eye movement and heading) measurements are reported relative to this point of origin. After the fixation phase the cross disappeared automatically and the dots (in case of the DC task) or the two cupboards (in case of the CVS task) became visible.

2.4. Subjects

Twelve homonymous visual field defect (HVFD) patients without visual neglect (age: 45.2 ± 16.1 mean ± SD, range: 22–71 years; see Table 1) and twelve normally sighted control subjects (age: 44.4 ± 15.8 mean ± SD, ages in ascending order: 20, 24, 27, 30, 40, 41, 42, 45, 50, 64, 65, and 66 years) participated in this study. Patients were recruited from the Department of Neuroophthalmology at the University of Tübingen (Germany), the University Neurology Clinic of Tübingen, as well as the Neurology Clinic of Burger Hospital in Stuttgart and the Bad Urach Rehabilitation Centre. All patients had normal function of the anterior visual pathways, as evaluated by orthoptic and ophthalmologic tests (fundus and slit-lamp examinations). Best corrected monocular visual acuity was at least 16/20 (near and far). Patients with unilateral visual hemi-neglect were excluded from the study by testing horizontal line bisection (Stone, Halligan, Wilson, Greenwood, & Marshall, 1991), copying of figures (Johannsen & Karnath, 2004), reading ability, and by means of the "Bells test" (Gauthier, Dehaut, & Joannette, 1989). Furthermore, the patients investigated in this study showed no evidence of cognitive decline, aphasia, apraxia, visual agnosia, or physical impairment. Clinical and demographic data of all patients are summarized in Table 1. After the visual field evaluation (see below) patients were interviewed about their everyday life difficulties using the standardized 25-item National Eye Institute (NEI) Visual Function Questionnaire (VFQ-25, version 2000; see Mangione et al., 1998, 2001). The NEI-VFQ-25 focuses on the influence of visual disability and visual symptoms on generic health and task-oriented domains related to daily visual functioning. The questionnaire includes twelve vision-targeted subscales (i.e. eleven subscales related to vision: global rating, difficulty with near activities, difficulty with distance activities, limitations in social functioning, role of limitations, dependency on others, mental health symptoms, driving difficulties, limitations with peripheral and color vision, ocular pain; and one general health rating item). Subscales are scored on a 0- to 100-point scale in which 100 indicated the best possible score on the measure and 0 the worst. The composite NEI-VFQ-25 score was the mean score of all items except for the general health item.

Normal-sighted control subjects were recruited from the Department of Neuroophthalmology at the University of Tübingen and were in many cases patients' relatives. They had normal or corrected to normal vision, normal-appearing fundus, normal visual fields, normal orthoptic status, and no physical or cognitive impairment. The research study was performed according to the Declaration of Helsinki and was approved by the independent ethics committee of the University of Tübingen (Germany). Following verbal and written explanation of the experimental protocol each subject gave their written consent, with the option of withdrawing from the study at any time.

2.5. Visual field evaluation and brain lesion analysis

Assessment of the patients' visual fields was carried out by monocular supraliminal automated static perimetry within 30°-area, binocular supraliminal automated static perimetry within 90°-area as well as binocular semi-automated 90° kinetic perimetry obtained with the OCTOPUS 101-perimeter (Fa. HAAG-STREIT, Koeniz, Switzerland). Visual fields of control subjects were assessed with binocular supraliminal automated static perimetry within 90°-area and binocular semi-automated 90° kinetic perimetry. A summary of all perimetric and MRI results of all patients is given in Table 7.

For analysis of the brain lesions, patients' lesions were mapped on normalized brain scans using MRIcro software (Rorden & Brett, 2000) and SPM5 (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm). MRIcro software was used to map the lesion on transversal slices of the T1-template MRI from the MNI (www.bic.mni.mcgill.ca/cgi/icbm_view) distributed with MRIcro. For anatomic analysis the left-sided lesions were mirrored and superimposed on the right side of the brain template. For each group of patients (i.e. $HVFD_I$ and $HVFD_A$), lesions were overlapped onto the template brain. Subtraction plots directly contrasted $HVFD_I$ and $HVFD_A$ patients. Since subtractions were made between groups of different sizes proportional values were used. Finally, mask analysis was performed in order to indicate regions that are more frequently damaged in $HVFD_I$ patients than in $HVFD_A$ patients.

Table 1
Clinical and demographic data of all 12 HVFD subjects.

Pat. ID	Sex	Age (year)	Δt (year)	Aetiology	Site/extent of lesion	Side of brain lesion	Type of HVFD	A-HVFD (deg^2)	A-SPAR (deg^2)	D (deg)	RT (ms)
ECG	Male	33	1	Brain surgery	Parieto-occipital	Right	Left cHH; mac. sparing	9559	414	3.2	1062
ANE	Male	40	4.9	Ischemia	Occipital	Right	Left cHH; mac. sparing	9258.9	923.7	2.3	299
AIH	Female	46	16	Ischemia	Parietal	Left	Right cHH; mac. sparing	9881	391	2.1	442
ULH	Male	64	0.7	Ischemia	Occipital	Right	Left upper iQA	2837	6790.6	7.8	348
FRH	Male	65	0.5	Ischemia	Occipital	Left	Right iHH; mac. sparing	7720.4	1986.6	15.4	518
URF	Male	71	1	Ischemia	Occipital	Left	Right iHH; mac. sparing	4739.4	4632	19	305
ARG	Female	36	11.2	Ischemia	Occipital	Left	Right cHH; mac. sparing	9003.3	1335	7	344
ARJ	Male	31	1.6	Hemorrhage (Aneurysm)	Parietal	Left	Right cHH; mac. sparing	10342.5	149.4	0	357
AYC	Female	33	1.1	Ischemia	Occipital	Left	Right cHH; mac. sparing	9370.8	845.5	4.5	260
TRH	Female	40	2.7	Ischemia	Occipital	Left	Right upper iQA	567.8	8853.2	4.7	311
TTC	Female	22	3.9	Ischemia	Parieto-occipital	Left	Right upper cQA	5867	4710.7	1.7	267
CKF	Male	61	3.6	Ischemia	Occipital	Right	Left upper iQA	2748.1	5496.4	8	387
Mean ± SD		45.2	4.02					6824.6	3044.0	6.3	408.3
		16.1	4.80					3358.6	2935.7	5.7	218.6

Δt – time since brain lesion and neuro-ophthalmological examination; Type of HVFD – characterization of homonymous visual field defect (HH: homonymous hemianopia, QA: quadrantanopia, c: complete, i: incomplete); A-HVFD – area of the visual field loss in the binocular visual field for stimulus III/4e; A-SPAR – area of the spared visual field in the affected hemifield for stimulus III/4e; D – minimum linear distance between the central fixation point and the defect border; RT – perimetric reaction time.

2.6. Data analysis and statistics

The MATLAB® software (MathWorks Company, Natick, USA) was used to analyze the recorded experimental data. Based on head and eye tracking data, the gaze vector was calculated in angles with an azimuth and an elevation component (α and β, respectively) with respect to the point of origin (see Fig. 2). Thus, the gaze vector includes both the head-in-space and the eye-in-head vectors. Object fixations were defined as sections of the gaze trajectory where gaze velocity did not exceed 100°/s for at least 120 ms. A gliding window procedure was used to distinguish such gaze fixations (stable gaze position related to the processed stimulus region) from gaze saccades (cf. Hardiess et al., 2008).

Task performance was quantified in terms of response times and error rates. In the DC task, error rate was defined as the unsigned difference of the reported and true dot number (20) in percent. In the CVS task, we distinguish two types of error, miss and false alarm, corresponding to a lower or higher number of reported targets than were actually presented. Misses and false alarms will be pooled to a total error rate.

To compare patient's ability to solve the two experimental tasks, a rank order was calculated based on the two task performance parameters response time and error rate independently. To get the final rank order, both rank numbers (i.e. for error rate and response time) were multiplied and the results of all 12 patients were ordered consecutively from 1 (i.e. best task performance) to 12 (i.e. worst task performance). In order to compare the patients task performance with their statements related to the quality of life questionnaire (VFQ-25; cf. Papageorgiou et al., 2007) the calculated final scores of the VFQ-25 were also ranked from 1 (i.e. best quality of life) to 12 (i.e. worst quality of life).

A distinction between adequate and inadequate patients was made with the median splitting method. Independently for each task both performance parameters (i.e. error rate and response time) were used to span a two dimensional co-ordinate system (see Figs. 3 and 4). All 12 data points from the patients' experimental performance were mapped into this system. The medians of both parameters were used to divide the co-ordinate system into four quadrants. Patients with error rate and response time above the respective medians (upper right quadrant) were assigned to the "inadequate" group while all remaining patients constitute the "adequate" group ($HVFD_I$ and $HVFD_A$, respectively). Contrary to previous grouping methods (cp. Zihl, 1995b, 1999), the median splitting approach employs an intrinsic criterion based on the patients' own data rather than on a comparison with the healthy subjects' performance. Only after separating patients into two groups the task performance comparisons between each of these groups and the control subjects were analyzed.

Parametric statistics were applied for the majority of the data. For some variables lacking standard distribution, data were transformed via $\log_{10}(x)$ operation to reach normally distributed values. For all other variables nonparametric statistics were applied.

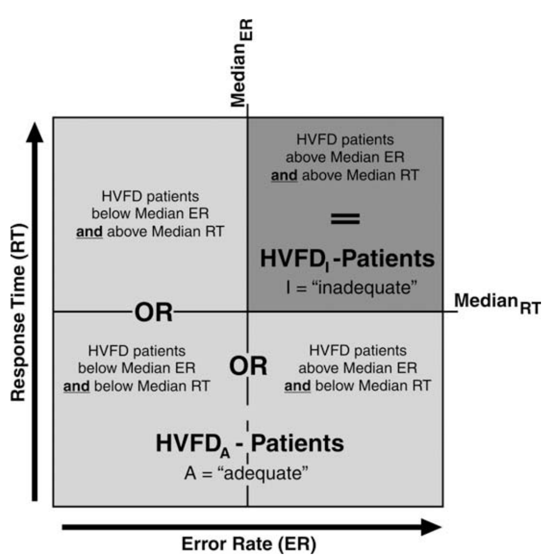


Fig. 3. Scheme for illustrating the median splitting method. The both task performance variables error rate and response time span a two dimensional co-ordinate system. Independently for each task the data of all 12 HFVD patients were added to this system. The medians of the patients data related to error rate and response time divide the sample into four quadrants. All patients whose data points are located into the quadrant labeled as above median ER and RT fall into the patients group called $HVFD_I$. All other patients are grouped to $HVFG_A$.

3. Results

3.1. Task performance analysis

3.1.1. Rank comparisons

The task performance values for all subjects represented by the parameters error rate and response time are plotted in Fig. 4. The dotted lines indicate the medians for error rate and response time of the homonymous visual field defect (HVFD) patients. Also the assigned rank number (from 1 to 12) determined independently for each task (see below) is plotted for each subject. Interestingly, the data distributions of patients and controls overlap to a great extend for the dot counting (DC) task. Only three patients performed with a higher error rate than controls whereas no differences regarding response time are apparent. In contrast, in the comparative visual search task (CVS), the data distribution of all control subjects was localized within the lower left quadrant. Hence, the overlap between patients and control was much less in this task (see Fig. 4, right side). Additionally, the data distribution of patients in the CVS paradigm showed an increased variance compared with the controls. In both tasks, the same four patients (ECG, ULH, ANE, and AIH) cluster in the upper right quadrant, leading to identical adequate and inadequate groups for both tasks. However, the two groups appear clearly separated in the CVS tasks whereas the patients' data in the DC task are organized rather continuously.

To enable a comparison between the homonymous hemianopes' task performance in the DC and in the CVS task, all 12 patients were ranked independently for each task (cf. Section 2.6). These ranks show a significant correlation (Rho-S = 0.63, $p < 0.05$; see Fig. 5). This analysis also confirms the definition of the "inadequate" group initially derived from the un-ranked performance data (grey disk in Fig. 5).

Fig. 6 shows the relation between functional deficits (task performance) and reported quality of life parameters (VFQ-25), expressed in terms of the respective ranks. For both experimental tasks, weak but not significant statistical relations were found (Rho-S = 0.48 for the DC task and Rho-S = 0.29 for the CVS task comparison).

3.1.2. Task performance comparisons

Interestingly, the group of $HVFD_A$ patients accomplished the DC task with the same performance level as control subjects, as judged from both, error rate and response time (see Fig. 7A and C). In contrast, statistical analysis confirmed that $HVFD_I$ patients performed significantly worse than controls with respect to error rate ($p < 0.05$, two-sided Mann–Whitney–U test; cf. Fig. 7A) and response time ($F(2, 60) = 6.32$, MSE = 11.63, $p < 0.01$, $\text{eta}_p^2 = 0.17$; post-hoc comparison between controls and $HVFD_I$ subjects, $p < 0.01$; cf. Fig. 7C). In the CVS task, the comparison between each

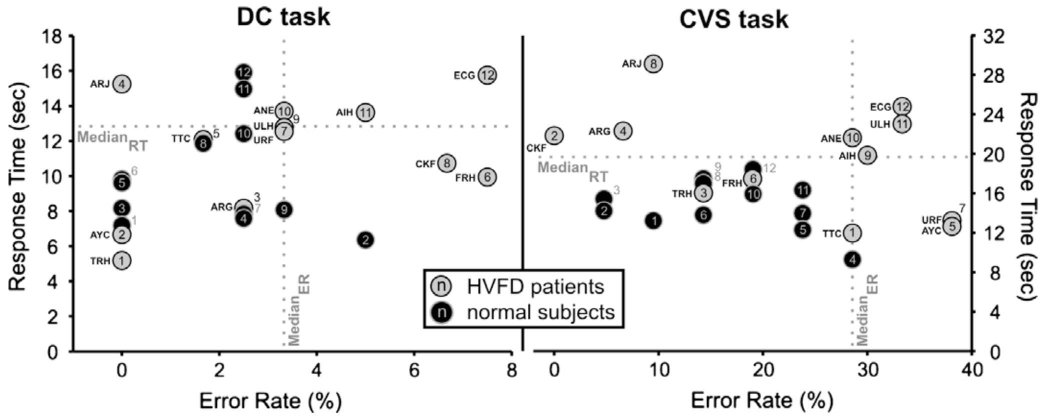


Fig. 4. The two task performance parameters error rate and response time plotted separately for each task (left: dot counting, right: comparative visual search) and for all subjects (grey circles: HVFD patients, black circles: normal subjects). The numbers within or beside each circle denote the given rank number calculated separately for each task and for the two subject groups. For reasons of comparison patients' labels are presented beside the circles.

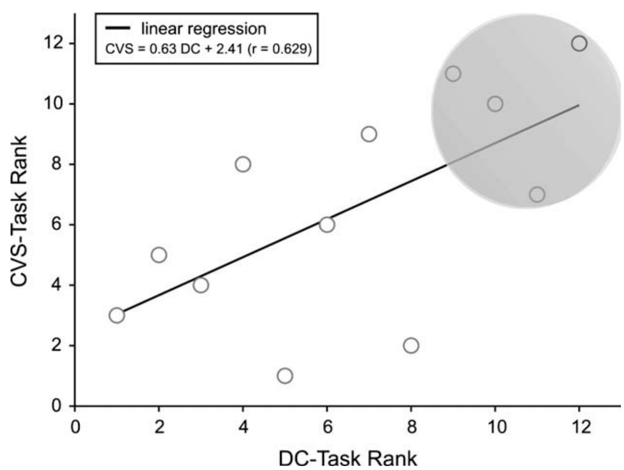


Fig. 5. Patients' task performance correlation based on the ranking method between the DC and the CVS task. Regression indicates a linear relation with a correlation coefficient $r = 0.63$. The four patients with the highest ranks in both tasks marked with the grey circle are indicated as inadequate patients ($HVFD_I$).

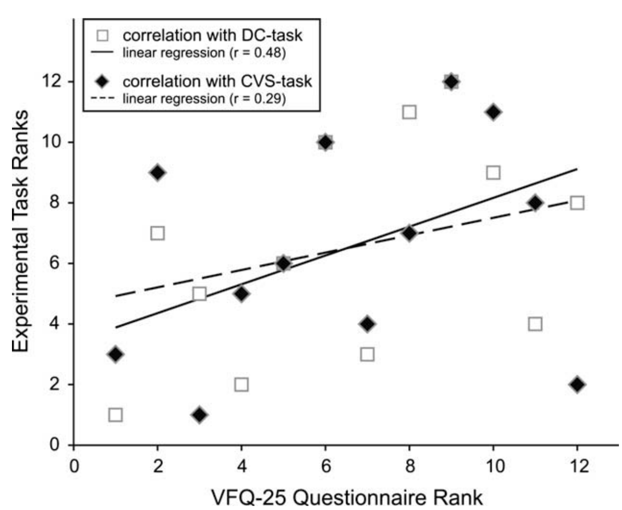


Fig. 6. Correlations between the patients' ranks due to the VFQ-25 questionnaire and their performance ranks in both experimental tasks (DC and CVS). Regressions indicate for weak relations with correlation coefficients $r = 0.48$ (correlation with DC-task) and $r = 0.29$ (correlation with CVS-task).

patient group and the controls showed that $HVFD_I$ patients made more errors than controls ($p < 0.01$, two-sided Fisher's exact test), whereas the error rate of $HVFD_A$ patients was similar to that of controls (see Fig. 7B). However, the analysis of variance of response time between the three subject groups revealed a significantly increased search time for the two patient groups ($F(2, 501) = 59.84$, MSE = 22.34, $p < 0.001$, $eta_p^2 = 0.19$; see Fig. 7D).

Tables 2 and 3 show the errors in more detail. For the DC task (Table 2), the normals tended to overcount the number of dots while both patient groups underestimate the dot number. This tendency is most pronounced in the $HVFD_I$ patients. Table 3 shows the proportions of different error types within the total number of errors for all groups concerning the CVS task. No obvious differences in error distribution were found between these groups. The most common error for all subjects was a miss error when in fact there were two targets presented. False alarm errors when no target was presented occurred fewest of all.

3.2. Scanpaths

The difference between $HVFD_A$ and $HVFD_I$ patients concerning task performance became also evident in their respective scanpath patterns. Fig. 8 shows representative recordings of individual scanning patterns in a normal subject, in a $HVFD_A$, and in a $HVFD_I$ patient for both tasks. In the DC task there are no apparent differences regarding the scanpaths between the normal subject and the adequately performing patient (see Fig. 8A and B). Both participants showed a systematic scanning behavior covering the stimulus field but not fixating each individual dot. In contrast, the $HVFD_I$ patient (cf. Fig. 8C) performed with a highly increased number of small saccades. The scanpath appears rather un-systematic and time-consuming. For the CVS task, similar differences were found (see Fig. 8D–F). However, due to a rather organized layout of the geometrical objects within the shelves, all subjects applied an overall structured search pattern. This pattern type was also apparent for the $HVFD_I$ patient (see Fig. 8F), but with a larger number of fixations and an increased positional scatter. In comparison, the $HVFD_A$ patient showed an organized scanning pattern similar to that of the unimpaired normal subject (cf. Fig. 8D and E).

3.3. Gaze performance analysis

3.3.1. Dot counting

To identify the strategies used for visual field compensation in both patient groups, relevant oculomotor parameters were calculated and compared with the data of the control group (Fig. 9).

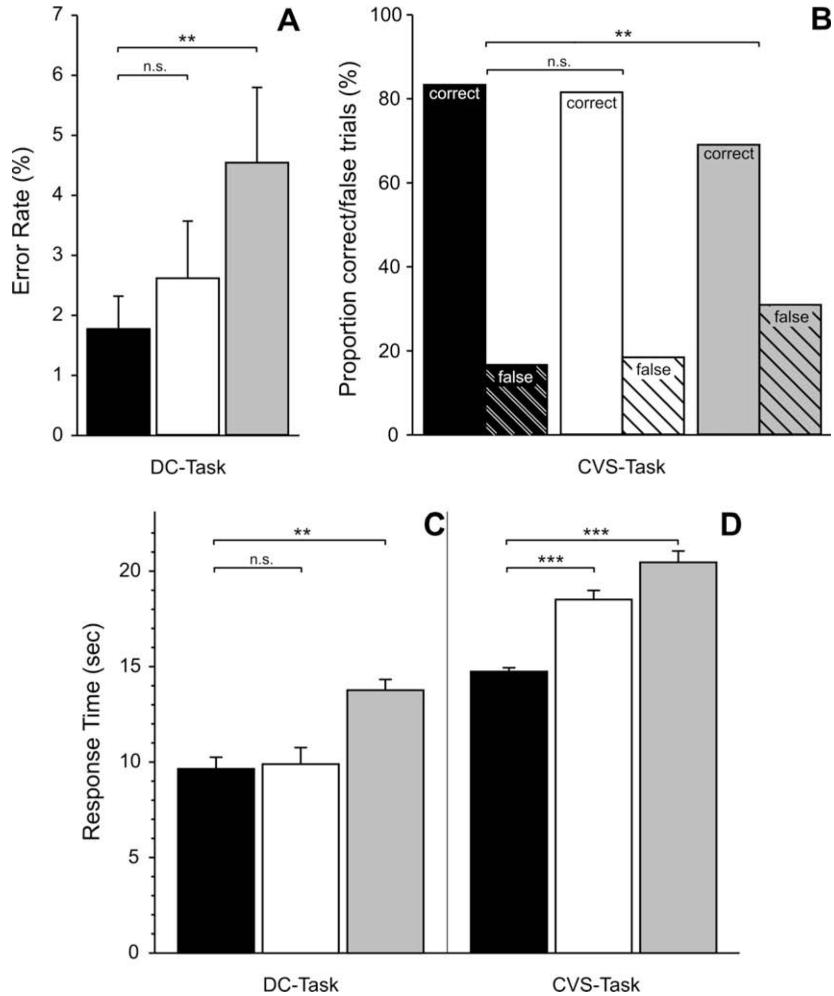


Fig. 7. Task performance comparison (A and B: error rate; C and D: response time) between normal subjects (black bars) and the $HVFD_A$ (white bars) respectively the $HVFD_I$ (grey bars) patient group. Post-hoc analysis was calculated to identify significance between the control subjects and each of the patients' group (Bonferroni: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and n.s. denotes not statistically significant). Error bars indicate standard error of the mean.

Table 2
Comparison of the type of counting errors (i.e. number of over- or undercounted dots in percent) in the DC task between controls, $HVFD_A$, and $HVFD_I$ patients.

Condition	Controls	$HVFD_A$	$HVFD_I$
# Dots overcounted per trial	0.30	0.19	0.27
# Dots undercounted per trial	0.06	0.33	0.64

For a better overview, all statistical results related to the analyzed oculomotor parameters are summarized in Table 4.

In comparison to normal controls, $HVFD_I$ patients showed an increased number of fixations (Fig. 9A), a higher proportion of fixations towards the impaired visual field (Fig. 9B), increased total scanpath length (Fig. 9C), and a higher proportion of refixations (calculated as the number of fixations made within 1° of an earlier one; Fig. 9D). Tendencies for increase fixation duration (Fig. 9E) and smaller saccadic amplitudes (Fig. 9F) are apparent but did not reach significance. In contrast to the $HVFD_I$ patients, $HVFD_A$ patients showed no significant differences from the normal controls in any of the investigated parameters.

3.3.2. Comparative visual search

For the CVS task, we considered the same gaze parameters as before, except for the fixation repetition rate which seems to be of little interest given the narrow spacing of target objects in the "shelves" stimulus. Instead, the number of gaze shifts between the two stimulus halves (cupboards) was evaluated as an indicator for working memory involvement (Fig. 10D). The statistical results for all gaze parameters are summarized in Table 5. Unlike the DC task, the cognitively more demanding CVS task leads to significant

Table 3
Comparison of the type of search errors (i.e. proportion of false alarm and miss trials due to the three target conditions in percent) in the CVS task between controls, $HVFD_A$, and $HVFD_I$ patients.

Condition	Controls		$HVFD_A$		$HVFD_I$	
	False alarm (%)	Miss (%)	False alarm (%)	Miss (%)	False alarm (%)	Miss (%)
Zero target trial	0.00	–	9.68	–	5.13	–
One target trial	7.69	30.77	16.13	22.58	20.53	17.95
Two target trial	–	61.54	–	51.61	–	56.41

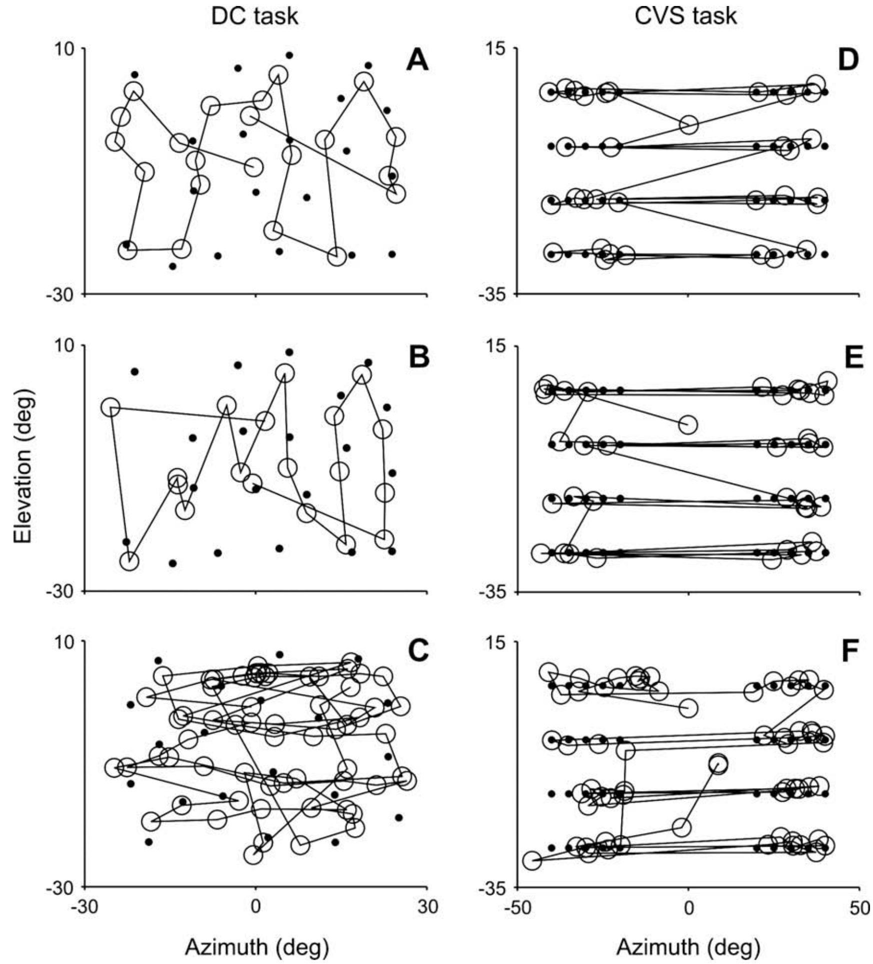


Fig. 8. Scanning pattern (scanpaths) examples for both tasks of a normal subject (A and D), of a $HVFD_A$ patient (B and E) and of a $HVFD_I$ patient (C and F). Black filled circles mark the dot position for the DC task and the object position for the CVS task. The open black circles indicate for the averaged gaze positions during fixations and the black lines illustrate the rapid gaze changes between fixations (saccades).

effects also for the $HVFD_A$ patients, including increased fixation number (Fig. 10A), increased scanpath length (Fig. 10C), and decreased saccadic amplitude (Fig. 10F). For the $HVFD_I$ patients, the effects of fixation number (Fig. 10A) and proportion of fixations to impaired visual field (Fig. 10B) are reproduced. As additional effects, we found increased fixation duration (Fig. 10E) and decreased saccadic amplitudes (Fig. 10F). For the scanpath length, the performance pattern of the three groups differed from the pattern found with the DC task. For this parameter, we found an increase in the $HVFD_A$ patients but not in the $HVFD_I$ patients (Fig. 10C). Here, the normal values for overall scanpath length together with the simultaneous increase in fixation number may be explained by the reduced number of long distance, inter-hemifield gaze shifts reported for the $HVFD_I$ patients but not for the $HVFD_A$ patients in Fig. 10D.

In the free-head comparative visual search task all subjects performed maximum head movements in a range of ±3° and ±20°. The average maximum amplitudes were larger for $HVFD_I$ patients (14.13 ± 8.0 mean ± SD), while for $HVFD_A$ patients they were within a range (8.89 ± 4.78 mean ± SD) similar to the one of normal subjects (9.12 ± 5.0 mean ± SD). Interestingly, all $HVFD_I$ patients showed significant differences for maximum head amplitudes to the left and right side (see Fig. 11). In more detail, the three left sided $HVFD_I$ patients (i.e. ECG, ANE, and ULH) used larger head movements to the left, while the only right sided $HVFD_I$ patient (AIH) displayed larger amplitudes to the right. This effect of different maximum head amplitudes between movements to the left and to the right could not be obtained for the majority of the $HVFD_A$ patients (see Fig. 11). Only three patients from this group (FRH, ARJ, and CKF) showed significantly different amplitudes but the effect sizes (between 0.62 and 0.82) were relatively low compared to those of the inadequate patient group (between 2.21 and 3.53). Five of the $HVFD_A$ patients showed no asymmetry in head movement amplitude.

3.4. Lesion analysis

Seven out of eight $HVFD_A$ patients had left-sided brain lesions, while three out of four $HVFD_I$ patients had right-sided brain lesions. MRI scans were available for six out of eight $HVFD_A$ patients and for three out of four $HVFD_I$ patients (see Table 7). In order to identify the anatomic structures that might be affected in $HVFD_I$ patients but spared in $HVFD_A$ patients, overlapping, subtraction and mask lesion analyses were performed using the MRIcro software (Fig. 12).

Fig. 12 illustrates simple lesion overlay plots for the group of $HVFD_A$ patients (Fig. 12A) and the group of $HVFD_I$ patients (Fig. 12B) respectively. In the subtraction analysis the superimposed lesions of the $HVFD_A$ group were subtracted from the $HVFD_I$ group, revealing percentage overlay plots (Fig. 12C). The focus of the subtracted lesion overlap (yellow and light orange) occurs at mesio-ventral areas of the temporal lobe (i.e. the fusiform gyrus)

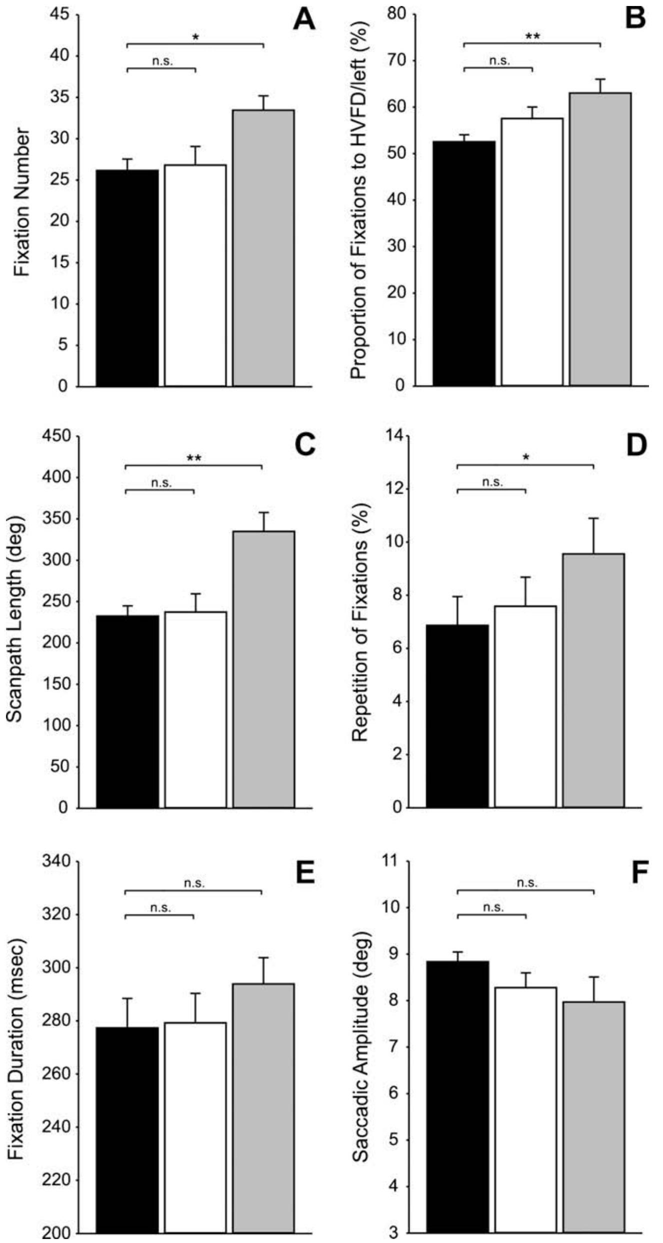


Fig. 9. Oculomotor performance of all subjects showed in the DC task. Comparisons were analyzed between the normal subjects (black bars) and the both patient groups (white bars: $HVFD_A$ patients, grey bars: $HVFD_I$ patients) related to different oculomotor parameters (A: number of fixations; B: proportion of fixations to the patients' impaired side or the control subjects' left side; C: length of the scanpath; D: percentages of repetition of fixations; E: duration of fixations; F: amplitude of saccades). Post-hoc analysis was calculated to identify significances between the controls and each of the patients' group (Bonferroni: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and n.s. denotes not statistically significant). Error bars indicate standard error of the mean.

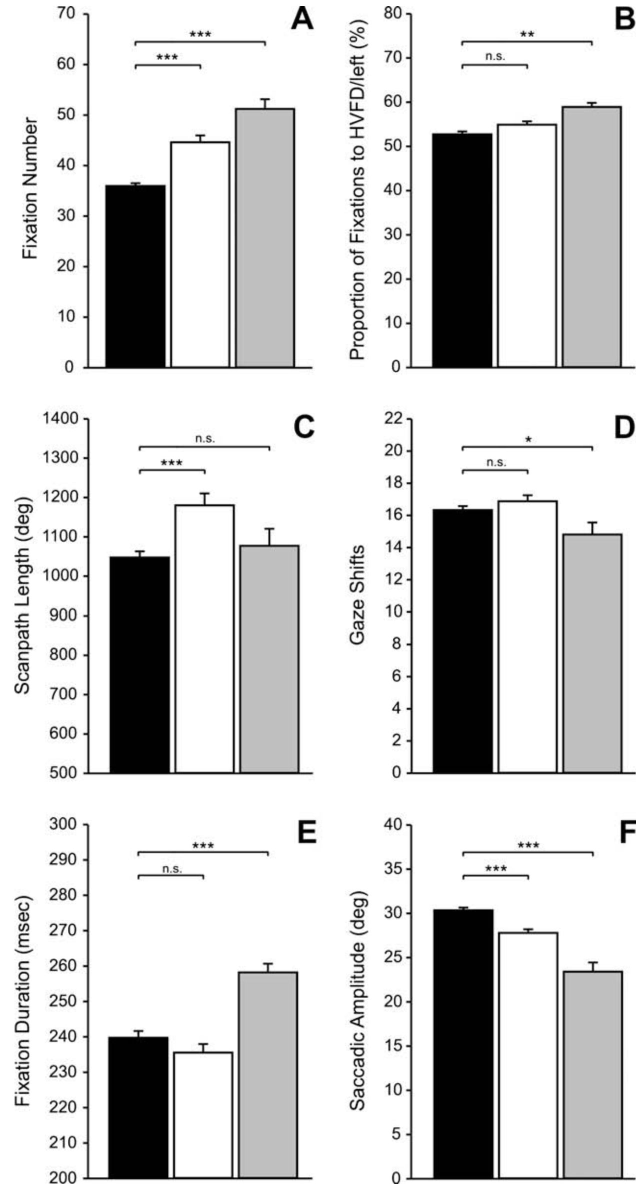


Fig. 10. Gaze performance of all subjects showed in the CVS task. Comparisons were analyzed between the normal subjects (black bars) and the both patient groups (white bars: $HVFD_A$ patients, grey bars: $HVFD_I$ patients) related to different gaze parameters (A: number of fixations; B: proportion of fixations to the patients' impaired side or the control subjects' left side; C: length of the scanpath; D: number of gaze shifts between the two cupboards; E: duration of fixations; F: amplitude of saccades). Post-hoc analysis was calculated to identify significances between the controls and each of the patients' group (Bonferroni: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and n.s. denotes not statistically significant). Error bars indicate standard error of the mean.

Table 4
Summary of the statistical results for all gaze performance parameters analyzed in the DC task.

Parameter	Statistical data	Significance
Fixation number[a]	$F(2, 60) = 4.18$, MSE = 0.014, $\text{eta}_p^2 = 0.12$	$p < 0.05$
Prop. of fixations to HVFD	$F(2, 60) = 5.07$, MSE = 94.725, $\text{eta}_p^2 = 0.14$	$p < 0.01$
Scanpath length[a]	$F(2, 60) = 7.32$, MSE = 0.017, $\text{eta}_p^2 = 0.2$	$p < 0.01$
Repetition of fixation	Median test: $\chi^2 = 6.07$	$p < 0.05$
Fixation duration	Median test: $\chi^2 = 2.98$	$p = 0.23$
Saccadic amplitude	$F(2, 60) = 1.97$, MSE = 1.938	$p = 0.15$

[a] This parameter was $\log_{10}(x)$ transformed to reach normally distributed values.

Table 5
Summary of the statistical results for all gaze performance parameters analyzed in the CVS task.

Parameter	Statistical data	Significance
Fixation number	$F(2, 462) = 44.2$, MSE = 177.43, $eta_p^2 = 0.16$	$p < 0.001$
Prop. of fixations to HVFD	$F(2, 462) = 12.93$, MSE = 85.04, $eta_p^2 = 0.053$	$p < 0.001$
Scanpath length	$F(2, 462) = 8.49$, MSE = 99446, $eta_p^2 = 0.035$	$p < 0.001$
Gaze shifts	$F(2, 462) = 5.02$, MSE = 21.7, $eta_p^2 = 0.021$	$p < 0.01$
Fixation duration[a]	$F(2, 462) = 17.89$, MSE = 0.0026, $eta_p^2 = 0.072$	$p < 0.001$
Saccadic amplitude	$F(2, 462) = 43.22$, MSE = 32.43, $eta_p^2 = 0.16$	$p < 0.001$

[a] This parameter was $\log_{10}(x)$ transformed to reach normally distributed values.

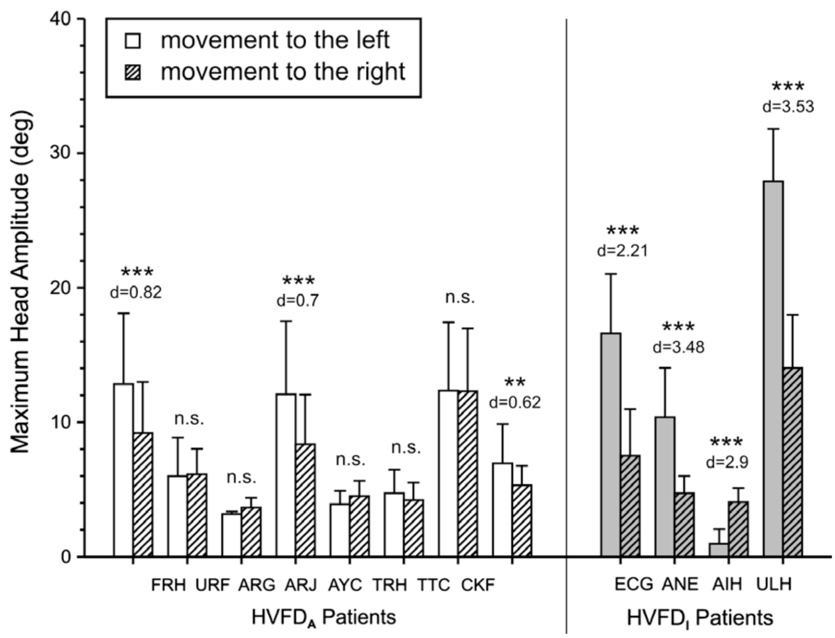


Fig. 11. Comparison of the averaged maximum amplitudes for horizontal head movements to the left (solid bars) and to the right side (striped bars) between the $HVFD_A$ (white bars) and $HVFD_I$ patients (grey bars) in the CVS task. Error bars indicate standard deviations. Statistical results for unpaired group comparisons are shown (unpaired *t*-tests: $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and n.s. denotes not statistically significant). The effect size of these statistics is marked as d.

and the inferior occipital lobe, that are damaged at least 60% more frequently in $HVFD_I$ patients than in $HVFD_A$ patients (Fig. 12C). The subsequent mask analysis, which identifies deficits that are unique to $HVFD_I$ patients, confirms this finding and reveals additional involvement of the parahippocampal gyrus (Fig. 12D).

4. Discussion

The purpose of the present study was to compare the compensatory gaze strategies of hemianopes occurring in two visual scanning tasks with different cognitive and visual processing demands. The results show (i) that patients can be grouped on the basis of task performance and that the assignment to the adequate and inadequate groups correlates between the different tasks; the performance level of the adequate group is not significantly different from that of normal controls. Grouping also correlates with the patients' brain lesions with more occipital lesion sites in the $HVFD_I$ patients. (ii) Compensatory gaze movements alone do not explain the performance differences between the two groups. In the dot counting (DC) task, $HVFD_I$ patients show longer and more detailed scanning behavior without reaching the performance level of normals or of $HVFD_A$ patients, who solve the task without obvious gaze adaptation. (iii) In the two tasks, different patterns of compensatory gaze movements are found. While $HVFD_A$ patients show no compensatory movement in the DC task, they turn to such behavior in the comparative visual search (CVS) task. $HVFD_I$ patients seem to switch to different compensation strategies in the CVS task. We suggest that this is related to an increased working memory involvement.

4.1. Differences in task performance among HVFD patients

Following the classification approach of Zihl (1995b, 1999) we divided the collective of HVFD patients into two groups (i.e. $HVFD_A$ and $HVFD_I$ patients; **A** = adequate task performance, **I** = inadequate task performance). But, instead of relating the patients' task performance to that of healthy controls (cf. Zihl, 1995b) or using their behavior in everyday life evaluated by questionnaires (cf. Zihl, 1999), we split up the patients based on their intrinsic task performance (i.e. error rate and response time) in both experiments. Interestingly, the majority of HVFD patients could reach adequate performance (i.e. $HVFD_A$ patients) and only 33% of our subjects were assigned to the $HVFD_I$ patient group. This is in line with the results from Zihl (1995b, 1999) who could identify a high number of adequately performing patients as well. In these investigations about one half of the subjects showed search times in the range

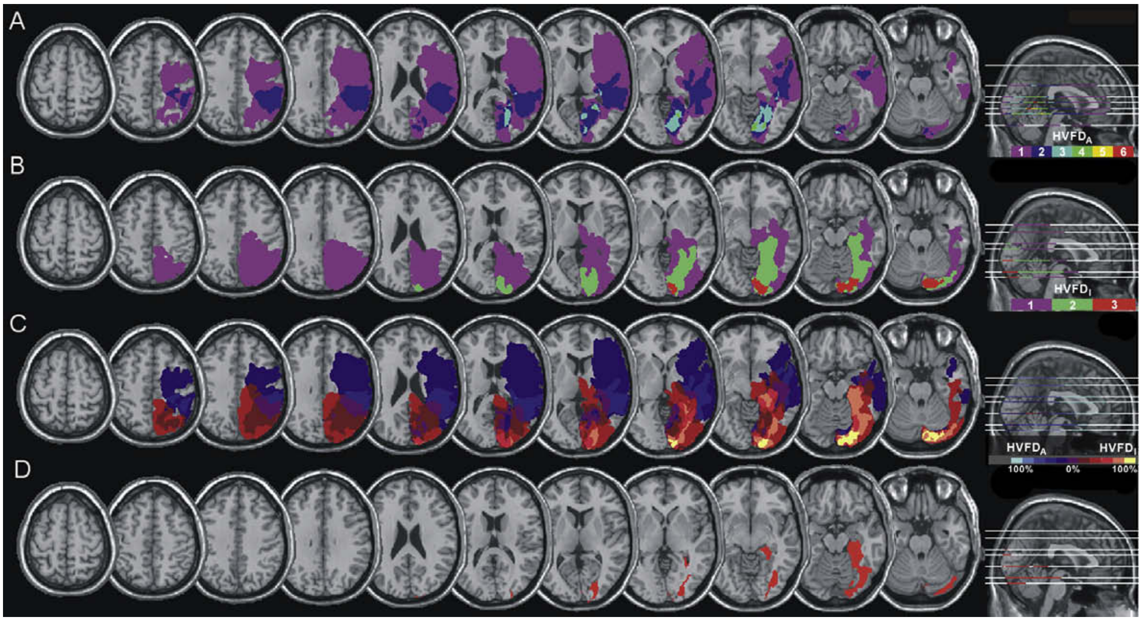


Fig. 12. Overlapping, subtraction and mask lesion analyses. The lesion overlay plots, show the degree of involvement of each voxel in the lesions of the group of $HVFD_A$ patients (A) and the group of $HVFD_I$ patients (B). Overlapping lesions are color-coded with increasing frequency, which indicates the absolute number of patients: from violet ($n = 1$) to red ($n = 6$) for $HVFD_A$ patients and accordingly from violet ($n = 1$) to red ($n = 3$) for $HVFD_I$ patients. (C) Subtraction of the superimposed lesions of $HVFD_A$ patients from the overlap image of the $HVFD_I$ patients. The center of the subtracted lesion overlap (yellow and light orange area) shows regions damaged at least 60% more frequently in $HVFD_I$ patients than in $HVFD_A$ patients. (D) Subtraction overlap and the subsequent mask analysis, which indicates regions that are unique to $HVFD_I$ patients, reveal that the occipitotemporal (fusiform) gyrus, the parahippocampal gyrus and parts of the inferior occipital lobe are commonly damaged in $HVFD_I$ patients but spared in $HVFD_A$ patients.

of healthy subjects or was labeled as "unimpaired" because of their almost normal behavior in everyday life. Our results confirm the general conclusion that hemianopics' oculomotor performance should be analyzed in relation to task performance.

The comparison of both patient groups with the task performance of the unimpaired healthy subjects suggests that $HVFD_A$ patients reached normal performance level at least in the DC task. In the CVS task, this group also performed in the range of normal controls with respect to error rates. The increased time requirements of this group was due to their compensatory gaze behavior during the comparative search, that is, a significantly elevated number of fixations and increased scanpath length (cf. Section 4.2). Error rates and search times of healthy subjects and $HVFD_A$ patients found in the present study are similar to those reported previously (cf. Tant et al., 2002; Zihl, 1995b, 1999). The group of $HVFD_I$ patients performed significantly worse than controls in both tasks. Still, the search times and errors rates reported here are smaller than those found in the studies mentioned above. This could be due to our small sample of only four inadequate patients.

Overall, the performance data supported the assumption that the CVS task was the more difficult one. The two data distributions of controls and patients in the DC task were overlapping widely. In contrast, the performance values (response time and error rate) of all controls in the more complex CVS task were below the respective medians of the patients' data distribution. Consequently, patients had more problems reaching normal performance levels in visual search than in dot counting.

The group assignments, derived from both response time and error rate, correlated highly both between these two measures and between the DC and CVS tasks; this hints towards a stable performance level across tasks for each patient. One reason for the task-independent performance could be the subject-specific use of effective compensatory strategies developed during everyday life tasks. Also, clinical and demographic characteristics could influence the ability to adequately perform the tasks. However, none of the demographic and clinical parameters listed in Table 1 was correlated with the task performance of the patients (data not shown). These findings are supported by other studies. Zihl (1999, 2000) concluded that the presence, time since and severity of the HVFDs could not sufficiently explain the observed deficit. Also Pambakian et al. (2000) analyzed a task concerning viewing of naturalistic pictures and found that neither the location nor the size of the visual loss correlates with any of the analyzed oculomotor parameters. Additionally, in an ongoing own study investigating the HVFD patients' performance in a dynamic collision avoidance task, none of the clinical or demographic parameters could explain the patients' task performance (Papageorgiou et al., Submitted for publication).

4.2. Task demands and compensation strategies

The interpretation of task specific compensatory gaze behavior has to take into account three questions: what are the processing steps needed to solve a given task, how are these steps affected by hemianopia, and to what extend can gaze movements help overcome these processing deficits. Both tasks, DC and CVS, require scanning the visual field for target objects. Additionally, in the CVS task, objects and local object configurations have to be memorized and compared among each other. For the scanning part, compensatory gaze movements are likely to show increased scanpath length, increased number of fixations, and reduced saccadic amplitudes. In order to compensate for recognition deficits, increased fixation durations and therefore reduced scanpath lengths can be expected (Hardiess et al., 2008).

In accordance with previous findings (Tant et al., 2002; Zihl, 1995b, 1999, 2000) we found no significant differences in any of the investigated gaze parameters between subjects from the $HVFD_A$ group and healthy subjects in the DC task. This is in spite of the larger stimulus size of 60° by 40° used in our study. $HVFD_I$ patients showed significantly increased gaze parameters, including

Table 6
Significance comparisons of all gaze performance parameters between the two patient groups and healthy subjects for both experiments ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, and n.s. denotes not statistically significant).

Gaze parameter	DC task (mean ± sem)			CVS task (mean ± sem)		
	Controls	$HVFD_A$	$HVFD_I$	Controls	$HVFD_A$	$HVFD_I$
Fixation number	26.2 (1.4)	26.8 (2.3)	33.5 (1.7)	36.0 (0.6)	44.6 (1.4)	51.2 (2.0)
Significance			n.s.	*	***	***
Scanpath length	232.5 (12.3)	237.4 (22.0)	335.0 (22.8)	1047.6 (15.5)	1180.0 (30.3)	1077.2 (43.1)
Significance			n.s.	**	***	n.s.
Saccadic amplitude	8.8 (0.2)	8.3 (0.3)	8.0 (0.5)	30.4 (0.3)	27.8 (0.4)	23.4 (1.1)
Significance			n.s.	n.s.	***	***
Fixation duration	277.4 (11.1)	279.3 (11.1)	293.9 (9.9)	30.4 (0.3)	27.8 (0.4)	23.4 (1.1)
Significance			n.s.	n.s.	n.s.	***
Prop. of fixations to HVFD	52.6 (1.5)	57.5 (2.5)	63.0 (3.0)	52.8 (0.6)	54.9 (0.7)	58.9 (0.9)
Significance			n.s.	**	n.s.	**
Repetition of fixation (DC)/gaze shifts (CVS)	6.9 (1.1)	7.6 (1.1)	9.6 (1.3)	16.3 (0.3)	16.9 (0.4)	14.8 (0.8)
Significance			n.s.	*	n.s.	*

number of fixations, proportion of fixations to the side of HVFD, scanpath length, and repetition of fixations (cf. Table 6).

A completely different result was obtained for the cognitively more demanding comparative visual search paradigm. Here, the group of adequately performing patients also showed significant differences in their gaze behavior as compared to controls (cf. Table 6). The number of fixations and the scanpath length were increased, while the mean amplitude of saccades was decreased. It seems that $HVFD_A$ patients adapted by performing more fixations within each cupboard (CVS hemifield) while executing the same number of inter-hemifield gaze shifts as the controls. In a study conducted by Martin, Riley, Kelly, Hayhoe, and Huxlin (2007), hemianopes also performed a cognitively demanding task, i.e. the assembling of wooden models. In this study, all patients showed performance parameters comparable with those of healthy subjects while no conspicuity due to saccade dynamics or spatial distribution of gaze were found. The authors suggest that in naturalistic situations, hemianopes may be able to compensate quite effectively for their visual loss, perhaps by more strongly relying on visuo-spatial memory. Since peripheral visual information, which guides saccade targeting, is missing, patients used more memory-guided saccades and look-ahead fixations. Furthermore, they fixated the target of an upcoming reach and apparently irrelevant locations more often than controls. Such behavior is thought to reflect increased updating of spatial information in visual working memory, on which homonymous hemianopes might rely to a greater degree than controls. Our results in the CVS task differ from the findings of Martin et al. (2007) in that compensatory gaze movements were found also in the $HVFD_A$ patients. Still, we suggest that the memory effects discussed above also play a role in the CVS task, most notably in the processing related to recognition of objects and object configurations. Gaze adaptations of the $HVFD_A$ patients are like to be related to scanning demands.

The CVS specific gaze adaptations found in the $HVFD_I$ patients can be divided in a subset related to scanning (i.e. increased number of fixations, increased proportion of fixations to deficit side and reduced saccadic amplitude) and a second subset consisting of a reduced number of inter-hemifield gaze shifts and longer fixation durations. This second pattern was also found in an earlier study on CVS gaze adaptations where different costs were associated with inter-hemifield gaze shifts (Hardiess et al., 2008). With this gaze strategy subjects increased the involvement of visual working memory to avoid gaze saccades while memorizing larger chunks of information. We therefore suggest that in the present study, $HVFD_I$ patients attempt to solve the CVS task also with increased working memory involvement. The fact that they don't succeed thus hints towards a working memory problem. Lesion evidence for working memory deficits will be discussed below (cf. Section 4.3).

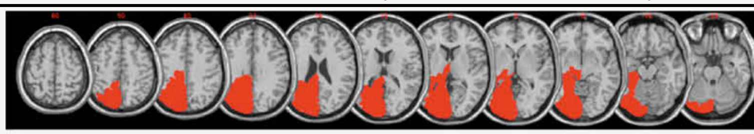
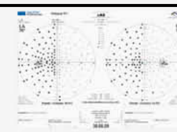
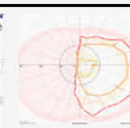
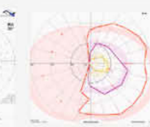
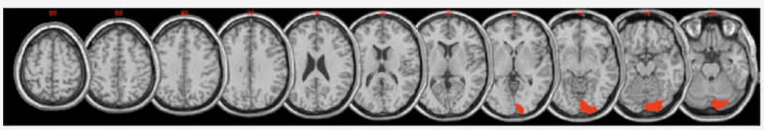
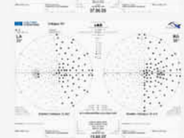
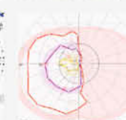
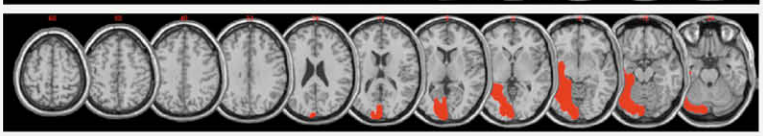
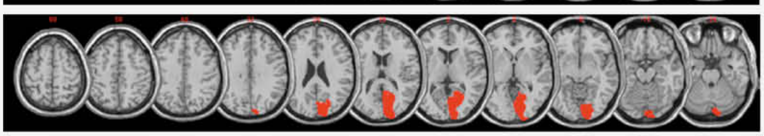
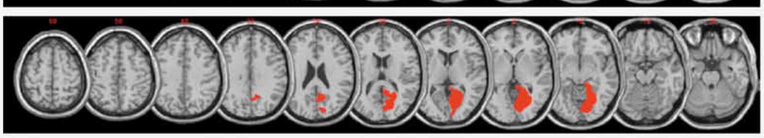
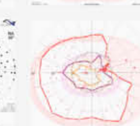
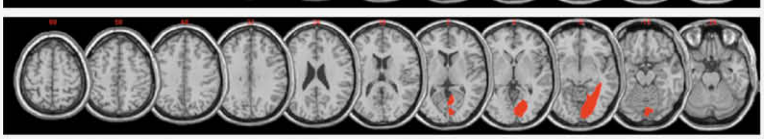
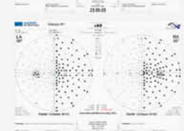
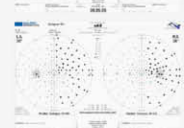
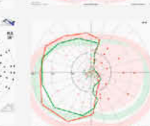
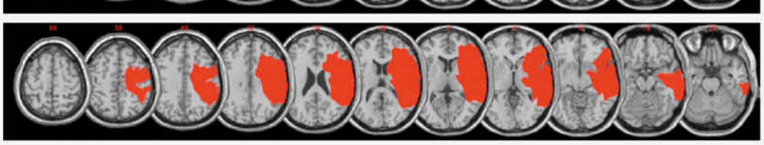
In conclusion, the gaze movement pattern reported here can be interpreted as follows: in the DC task, adequate patients perform on the level of normals without gaze movement compensation. We therefore assume that this compensation is brought about by increased working memory involvement. Inadequate subjects attempt compensation by gaze movements suitable for scanning tasks, but still do worse than the adequate patients, presumably due to insufficient working memory use. In the CVS task, compensation for both scanning and object recognition components must be achieved. Adequate patients use compensatory gaze movements of the scanning type and are thus able to reach normal performance levels. It can therefore be assumed that the effect of HVFD on object recognition is again compensated by working memory processes. If it is true that inadequate patients suffer from working memory deficits, they might attempt to compensate for both, scanning and recognition deficits simultaneously, thereby producing a novel pattern of gaze movement adaptations.

With respect to head movements in HVFD patients, previous studies reported smaller head movement proportion in combined head-eye saccades (Zangemeister, Dannheim, & Kunze, 1986; Zangemeister et al., 1982; Schoepf & Zangemeister, 1992, 1993). It was argued that head movement programming, which is more complex than eye movement programming alone, takes more time for HVFD patients. Consequently, the head movement proportion is reduced due to a malfunctioning coordination of the eye and head. In contrast, we found in the head unrestricted CVS task, that head amplitudes of $HVFD_A$ patients were within the same range as those of healthy controls (i.e. about ±9.0°). Furthermore, the group of $HVFD_I$ patients used a wider range of head movements (i.e. about ±14.0°). Interestingly, the proportion of head movement towards the impaired hemifield was larger in the $HVFD_I$ patients than in the $HVFD_A$ patients. One difference in experimental design that might account for the results from our and previous studies may be the large stimulus area used for the CVS task (i.e. up to ±45°). In any case, we suggest that HVFD patients use head movements in order to achieve additional compensation in a task specific manner.

4.3. Brain lesions and lateralization effect

We found a tendency for a lateralization effect related to the task performance between both HVFD patient groups. All except one patient in the poorly performing $HVFD_I$ group have lesions in the right brain hemisphere. However, this hemisphere is affected

Table 7
Magnetic resonance images (MRIs) of the head, monocular supraliminal automated static perimetry within 30°-area, and binocular semi-automated 90° kinetic perimetry obtained with the OCTOPUS 101-perimeter of all 12 HVFD patients. For three patients MRI data are not available.

Pat. ID	Head MRIs	Perimetry	
	Talairach z-coordinates: 60 50 40 32 24 10 8 0 -8 -10 -24	30°-NO	90°-SKP
ECG			
ANE	MRI data not available		
AIH			
ULH			
FRH			
URF			
ARG			
ARJ			
AYC	MRI data not available		
TRH			
TTC			
CKF	MRI data not available		

in only one of the $HVFD_A$ patients. Similarly, other studies indicated that patients with right-hemispheric lesions do less well on performance measures and driving tasks (Korner-Bitensky, Mazer, & Sofer, 2000; Mazer, Korner-Bitensky, & Sofer, 1998; Meerwaldt & Van Harskamp, 1982). In a dot counting paradigm Tant et al. (2002) reported that patients with left-sided hemianopia had increased error rates and search times. This lateralization effect was also visible in healthy subjects with simulated visual field loss, indicating that lateralization is not a result of lateralized brain damage. Therefore, the role of lateralization for visual scanning deficits remains elusive.

Zihl (1995b) suggested that the variability in HVFD compensation depends on the extent of brain injury and that parieto-occipital and posterior thalamic lesions may be responsible for insufficient compensation. On the other hand, Tant et al. (2002) observed clear parallels between simulated and real homonymous hemianopes, suggesting that hemianopic scanning behavior is primarily visually elicited, namely by the HVFD, and not by the additional brain damage. However, both studies refer to a simple laboratory task, i.e. dot-counting. For cognitively more demanding tasks, such as CVS or block assembly (Martin et al., 2007), an involvement of other brain regions, especially regions dealing with visuo-spatial memory, seems possible.

In our study, performance differences between $HVFD_I$ and $HVFD_A$ patients were much higher in the CVS than in the DC task. The inadequately performing patients have more difficulties in solving the more complex visual search task. Concerning visual processing there is clear evidence in the literature that spatial working memory performance interferes with visual search. This could be shown for the visuo-spatial sketchpad as part of working memory (Oh & Kim, 2004; Soto & Humphreys, 2008; Woodman & Luck, 2004) as well as for the central executive component (Han & Kim, 2004; Peterson, Beck, & Wong, 2008). Furthermore, results from other groups demonstrate that damage to the right posterior parietal cortex (rPPC) leads to a generalized deficit in visual working memory across a range of stimuli and encoding tasks (see Berryhill & Olson, 2008; Smith & Jonides, 1998; Todd & Marois, 2004). These results seem to suggest that the $HVFD_I$ patients' particularly poor performance in the CVS task might be due to an impairment of their spatial memory resulting from lesions of the rPPC. However, we found a rPPC lesion only in one (ECG) of the four $HVFD_I$ patients. The other $HVFD_I$ patients have visual field defects based on occipital lesions (ANE and ULH) or the left parietal region (AIH). Thus, the lesion analysis does not support the assumed role of spatial memory for the inadequate performance of this group of patients.

A further anatomical analysis identified three lesion sites as unique to $HVFD_I$ patients: mesio-ventral areas of the temporal lobe (i.e. the fusiform gyrus), the inferior occipital lobe, and the parahippocampal gyrus. Regarding the site of brain lesion, our results are consistent with a recent study on hemianopes in visual search (Machner et al., 2009), which showed that mesio-ventral areas of the temporal lobe were damaged in at least half of the severely impaired patients but spared in the mildly impaired patients. Temporal regions belong to the ventral processing visual stream, thought to be involved in the visual recognition of objects, including color, texture and form information (Ungerleider & Mishkin, 1982) and may also play a role in the control of attention (Goodale & Milner, 1996; Ungerleider & Pasternak, 2004).

Lesions of the mesio-ventral temporal areas and V4 might have affected object recognition and subsequently visual search of $HVFD_I$ patients as also suggested by Machner et al. (2009). Disturbance of attentional modulation within the ventral processing stream and damage of its connections with temporal lobe areas and the prefrontal cortex might be a further reason for impaired visual search, through deficits in visuo-spatial memory. In addition, we found that the parahippocampal gyrus is commonly affected in $HVFD_I$ patients. Since the parahippocampal gyrus serves as the main input–output pathway between the hippocampus and cortical association areas, its damage can lead to many cognitive deficits including deficits in memory storage or retrieval from other brain areas.

However, these findings are still subject to interpretation, because our lesion-mapping analysis has some limitations. First, our results are derived from a small number of patients with available MRI scans and the two groups of patients had unequal sizes. Secondly, the brain lesions were mirrored onto the right hemisphere (as in the study of Machner et al., 2009), in order to perform overlapping and subtraction analysis in a greater number of patients. However, the side of the brain lesion, as suggested by many studies and our results above (lateralization effect), might be decisive when studying visual exploration. Therefore, analysis in a larger group of patients separately for right- and left- sided lesions is needed. Yet, our findings are in accordance with previous studies which suggested that the occipitotemporal gyrus, and presumably the parahippocampal gyrus, might be involved in disturbances of visual search after unilateral vascular brain damage.

5. Conclusions

By analyzing the adaptive gaze behavior of patients with HVFDs, we identified two groups of patients differing in their capability to solve two different visual scanning tasks. The $HVFD_A$ patients spontaneously and adequately compensate for their visual field loss in the cognitively unchallenging sampling task as well as in the more demanding comparative visual search task. Although their oculomotor parameters in the DC task did not differ from those of healthy subjects, the $HVFD_A$ patients' gaze (eye and head movement) behavior showed increased compensational adaptations in the CVS task. For the inadequately performing patients (i.e. $HVFD_I$ patients) the pattern of compensational gaze movements differed from the $HVFD_A$ patients' pattern. Still, regardless of their increased adaptations, these patients failed to perform the two scanning tasks as accurately as controls or adequate patients.

We suggest that the difference between adequately and inadequately performing patients is due to reduced working memory availability in the $HVFD_I$ patients. In the DC task $HVFD_I$ patients therefore need to compensate with eye movements whereas $HVFD_A$ patients can rely on working memory. In the CVS task, working memory is needed for object recognition, such that scanning compensation now has to be achieved via gaze movements also in $HVFD_A$ patients. The $HVFD_I$ patients attempt to compensate by gaze movements for both, scanning and recognition demands, but fail. In terms of cortical lesions, losses unique for $HVFD_I$ patients are found mostly in the ventro-mesial temporal lobe.

In general, we argue that comparative studies using visual tasks with varying processing demands are needed to understand gaze movement behavior in hemianopes. Such tasks will require realistic, large field stimulus displays and simultaneous measurements of head and eye movements.

Acknowledgments

The authors thank the Rehabilitation Centre Bad Urach, the Neurology Clinic of Burger Hospital in Stuttgart and the European Union (PERACT – Marie Curie Early Stage Training MEST-CT-2004-504321) for their support for this study. We also thank the anonymous reviewers for their constructive criticisms and comments.

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ISSN 0042-6989 | Volume 52 | Issue 1 | 1 January 2012

Vision Research 52 (2012) 20–30

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Collision avoidance in persons with homonymous visual field defects under virtual reality conditions

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ARTICLE INFO

Article history:
Received 18 December 2010
Received in revised form 3 October 2011
Available online 12 November 2011

Keywords:
Homonymous visual field defects
Collision avoidance
Virtual reality
Cerebrovascular lesion
Aging

ABSTRACT

The aim of the present study was to examine the effect of homonymous visual field defects (HVFDs) on collision avoidance of dynamic obstacles at an intersection under virtual reality (VR) conditions. Overall performance was quantitatively assessed as the number of collisions at a virtual intersection at two difficulty levels. HVFDs were assessed by binocular semi-automated kinetic perimetry within the 90° visual field, stimulus III4e and the area of sparing within the affected hemifield (A-SPAR in deg^2) was calculated. The effect of A-SPAR, age, gender, side of brain lesion, time since brain lesion and presence of macular sparing on the number of collisions, as well as performance over time were investigated. Thirty patients (10 female, 20 male, age range: 19–71 years) with HVFDs due to unilateral vascular brain lesions and 30 group-age-matched subjects with normal visual fields were examined. The mean number of collisions was higher for patients and in the more difficult level they experienced more collisions with vehicles approaching from the blind side than the seeing side. Lower A-SPAR and increasing age were associated with decreasing performance. However, in agreement with previous studies, wide variability in performance among patients with identical visual field defects was observed and performance of some patients was similar to that of normal subjects. Both patients and healthy subjects displayed equal improvement of performance over time in the more difficult level. In conclusion, our results suggest that visual-field related parameters per se are inadequate in predicting successful collision avoidance. Individualized approaches which also consider compensatory strategies by means of eye and head movements should be introduced.

1. Introduction

Homonymous visual field defects (HVFDs), the loss of the field of vision in the same relative position in both eyes, are among the most frequent disorders after unilateral injury of the postchiasmatic visual pathway. Nearly 80% of patients with unilateral postchiasmatic brain lesions suffer from HVFDs (Zihl, 1995). Most common causes of HVFDs are strokes and, to a lesser extent, traumatic brain injury and tumors (Zihl, 2000). HVFDs create a marked amount of subjective inconvenience in everyday life (Gall et al., 2009; Papageorgiou et al., 2007). Patients with HVFDs may show persistent and severe impairments of reading, visual exploration and navigation, collide with people or objects on their blind side and may be deemed unsafe to drive (Trauzettel-Klosinski & Reinhard, 1998; Zihl, 2000, 2003). This has led to the belief that homonymous visual field loss is per se associated with functional impairment.

Driving has been considered to be problematic for patients with HVFDs; therefore researchers have assessed driving performance of patients with HVFDs in comparison to subjects with normal visual fields either in driving simulators or in on-road experiments. The few studies assessing the performance of patients with HVFDs in realistic or experimental driving paradigms report a variety of findings. Some authors suggest that performance of patients with HVFDs is significantly worse than that of normal subjects (Table 1, Bowers et al., 2009; Kooijman et al., 2004; Lövsund, Hedin, &

Abbreviations: HVFD, homonymous visual field defect; VR, virtual reality; A-SPAR, area of sparing within the affected hemifield; HH, homonymous hemianopia; QH, homonymous quadrantanopia.

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doi:10.1016/j.visres.2011.10.019

Table 1
List of studies assessing performance of patients with HVFDs (in descending chronological order).

Author	Study participants	Experimental setup	Results	Remarks
Wood et al. (2011)	22 patients with HH 8 patients with QH 30 controls	On-road test (interstate and non-interstate)	Patients rated as safe made larger eye movements and more head movements into their blind hemifield	Eye and head movements were assessed qualitatively by means of video footage, rather than by using a formal eye and head tracker system
Bowers et al. (2010)	12 patients with HH 12 controls	Driving simulator	Drivers with HH took a lane position that increased the safety margin on their blind side	Absolute lane position varied as the steering maneuver and location of the risk from oncoming traffic changed with road segment type
Hardiess et al. (2010)	12 patients with HVFDs 12 controls	Virtual reality (dot counting task and comparative visual search task)	8/12 patients could reach adequate performance in both tasks	In the two tasks, different patterns of compensatory gaze movements were found
Bowers et al. (2009)	12 patients with HH 12 controls	Driving simulator	HH drivers had significantly lower pedestrian detection rates on the HH-side	Wide variability among subjects and age the main factor for that. The relationship of simulator-based measures to on-road performance has yet to be established
Wood et al. (2009)	22 patients with HH 8 patients with QH 30 controls	On-road test (interstate and non-interstate)	73% of HH and 88% of QH patients received safe ratings	10 HH and 1 QH patients did not drive on the interstate, 44% of initially eligible patients did not participate in the study
Bowers, Keeney, and Peli (2008)	43 patients with HH	Follow-up questionnaires evaluating functional benefits for mobility	47% of patients were wearing the prism glasses after 12 months reporting significant benefits for obstacle avoidance	Objective measures of functional performance with and without prisms and a control or comparison treatment were not included
Martin et al. (2007)	3 patients with HH 4 controls	Naturalistic task (assembly of wooden models on a table)	No significant differences in task performance, saccade dynamics, spatial distribution of gaze	Small sample
Szlyk et al. (2005)	10 patients with HH due to occipital lobe lesions	Comparison of Fresnel prisms and Gottlieb system in the laboratory, on-road and in a simulator	Prism lenses and training in their use improved performance on visual functioning and driving-related skills	Need for data on the long-term safety of peripheral enhancement devices while driving
Racette and Casson (2005)	13 patients with HH 7 patients with QH	Retrospective chart review of occupational therapists' assessments of on-road driving test	Localized visual field loss (VFL) in the left hemifield and diffuse VFL in the right hemifield associated with impaired performance, patients with QH received no unsafe ratings	No control group, different therapists, retrospective design, lack of standardized route
Kooijman et al. (2004)	28 patients with HVFDs	On-road driving test pre- and post-training on a driving simulator	Only 4/28 patients with HVFDs passed the on-road test	No control group, referral of patients due to suspected driving safety concerns
Tant et al. (2002)	28 patients with HH	On-road driving test and neuropsychological visuospatial test performance	Only 14% of patients passed the test	Recruitment of patients whose driving was suspected to be unsafe by the caregiver or the patients themselves
Schulte et al. (1999)	6 patients with HVFDs 10 controls	Driving simulator	No differences in performance (driving speed, driving error rate, reaction time)	Small sample, restricted field of view (16° × 21°), few unexpected events
Zihl (1995)	60 patients with HH 16 controls	Dot counting task on a screen	40% of patients showed normal scanning behavior	Time since brain damage was at least 6 weeks
Szlyk, Brigell, and Seiple (1993)	6 patients with HVFDs 7 age-matched controls 31 younger controls	Driving simulator	Performance of patients worse than or similar to the older control group	3 patients had hemi-neglect, the study was performed 2 months after stroke
Lövsund, Hedin, and Törnros (1991)	26 patients with HVFDs 20 controls	Detection of static stimuli in a driving simulator at 24 positions	Only 3/26 patients with HVFDs were found able to compensate	Wide variation in the individual reaction time

Törnros, 1991; Szlyk, Brigell, & Seiple, 1993; Tant et al., 2002). On the other hand, other studies report that there are no performance differences between patients with HVFDs and control subjects (Table 1, Martin et al., 2007; Schulte et al., 1999; Wood et al., 2009). The majority of studies have highlighted poor steering control, incorrect lane position and difficulty in gap judgment as the primary problems of drivers with HVFDs (Bowers et al., 2009, 2010; Szlyk, Brigell, & Seiple, 1993; Tant et al., 2002; Wood et al., 2009). An additional question concerned the underlying factors affecting performance of patients with HVFDs. It has been a matter of debate whether driving performance of patients with longstanding HVFDs is primarily determined by visual field measures, e.g. the extent of the visual field along the horizontal meridian, the Esterman score (Johnson & Keltner, 1983), or affected by additional factors, such as aging, side of brain injury and compensation by eye and head movements (Pambakian et al., 2000; Wood et al., 2011; Zihl, 1995).

Rather than making general statements on the average performance of patients with HVFDs, recent evidence suggests that functional assessments to evaluate each patient individually should be introduced, because a significant portion of patients have the potential to compensate and wide variability among them occurs (Bowers et al., 2009; Hardiess et al., 2010; Wood et al., 2009, 2011). In order to enable individual assessments in driving scenarios, it has been argued that studies should address specific questions at specific road segments and in relation to specific visual impairments (Mandel et al., 2007). One aspect of driving behavior, which has not been studied adequately, is performance of patients with HVFDs at intersections. Hence, Bowers et al. (2009) investigated detection of stationary pedestrians at intersections and along the roadside on city and rural roads in a driving simulator, and found that HH (homonymous hemianopia) drivers exhibited significantly lower pedestrian detection rates on their blind side at intersections. However, collision avoidance ability of patients with HVFDs at intersections, in terms of detecting and appropriately responding to dynamic collision-relevant obstacles (i.e. cross-traffic vehicles), has not been studied yet.

Therefore, the aims of the present study were (i) to assess the performance of patients with HVFDs in comparison to normal-sighted control subjects in a dynamic collision avoidance task while crossing an intersection, and (ii) to investigate whether their performance can be explained by visual field indices. We evaluated performance of patients with longstanding HVFDs due to cerebrovascular lesions, in a collision avoidance task under virtual reality (VR) conditions and compared them to normal-sighted age-matched subjects. We hypothesized that patients with HVFDs would demonstrate poorer performance in terms of collision avoidance at an intersection. In particular, we expected that patients would collide more often with vehicles on the blind than the seeing side and there would be no difference in collision rates between the seeing side of patients and the normal-sighted subjects. However, we speculated that performance would not be solely explained by visual field-related parameters and therefore expected contribution of additional factors, e.g. age, side of brain lesion and time span since lesion onset. Literature on spatial cognition often reports gender differences, with males typically performing better in tasks involving mental rotation, three-dimensional figures and spatial orientation (Voyer, Voyer, & Bryden, 1995; Wolf et al., 2010). Therefore the effect of gender on collision avoidance was also investigated.

A driving scenario was chosen as a paradigm that concerns a familiar everyday situation. Driving consists of several subtasks (e.g. steering and lane positioning, visual exploration of the scenery, navigational considerations). However, we have isolated one central aspect, namely collision avoidance while crossing an intersection, in order to systematically address one type of error and the relevant visual requirements. Furthermore, collision avoidance is associated with daily living tasks such as crossing a road, walking in a crowd, or driving through an intersection, which often require pedestrians and drivers to adapt their behavior to the displacement of other objects in their environment (Lobjois et al., 2008). At an intersection, a driver must estimate the time interval that it will take for his car to cross the road before an oncoming vehicle will arrive there (i.e. time-to-contact, TTC) (Lobjois, Benguigui, Bertsch, & Broderick, 2008; Matsumiya & Kaneko, 2008; Schiff & Detwiler, 1979; Schiff & Oldak, 1990). This task requires oculomotor adaptation, head movements and visuo-motor calibration, which consists of perceiving the size of the gap between the cross-traffic vehicles in terms of time to (re)act (Lee, 1976; Simpson, Johnston, & Richardson, 2003). Yet the effect of homonymous visual field loss on the completion of such a cognitively challenging task has not been assessed previously.

Virtual reality was used in order to achieve standardized, repeatable and completely programmable experimental conditions and avoid any safety concerns and driving licensure issues that may be encountered in on-road studies. In contrast to a real driving scenario, we simplified our task by omitting steering, lane positioning, and navigational considerations. Here, only the active avoidance of a potential collision while approaching an intersection with variable number of cross-traffic vehicles has to be accomplished. The intersection task was constructed so as to enable simulation of all possible scenarios that may occur in reality (i.e. two lanes for traffic vehicles moving in opposite directions, variability in traffic density, speed control of the approaching car, a large field of view for the subjects, and scanning of the scenery by means of head and eye movements). In order to enable comparability between subjects we allowed speed adjustments within defined limits (i.e. no infinite acceleration and deceleration were possible) and we restricted the velocity of the cross-traffic vehicles to a fixed value. Usually (in real traffic scenarios), drivers can and have to stop in front of an intersection in order to prepare passage through the intersection when all other vehicles are out of the time-to-collision range. Clearly, this circumstance is not satisfied in our experimental design due to the need for detecting performance differences between study participants. However, our subjects never felt uncomfortable or overwhelmed with this adaptation. Additionally, the available period to react at an intersection is not always unlimited even in real world, because different categories of road users interact in these limited areas with crossing trajectories. The result is that in 2007 at least 22% of fatal accidents in the USA occurred at intersections (Fatality Analysis Reporting System Encyclopedia, 2007). Therefore, we believe that our intersection task is an adequate representation of the type of situation people face at (real) intersections.

2. Materials and methods

2.1. Subjects

Potential participants with hemianopia or quadrantanopia were recruited from the Department of Neuro-Ophthalmology and the Neurology Clinic at the University of Tübingen (Germany), as well as the Neurology Clinic of the Bürger Hospital in Stuttgart and the Bad Urach Rehabilitation Center. Normal-sighted control subjects were recruited from the Tübingen region and comprised group-age-matched volunteers from friends and relatives of the authors, the staff and the patients in the Department of Neuro-Ophthalmology at the University of Tübingen.

To be included in the study, all participants were required to be at least 18 years old, to have best corrected monocular (near and distant) visual acuity of at least 20/25 and normal function and morphology of the anterior visual pathways as evaluated by ophthalmological tests (fundus and slit-lamp examinations, ocular alignment, ocular motility). The group-age-matched control subjects should additionally have normal visual fields and no history of brain injury, physical or cognitive impairment. Patients should have a homonymous visual field defect, varying from complete homonymous hemianopia to homonymous paracentral scotomas, due to a unilateral vascular brain lesion, which was documented by neuroradiological examinations (magnetic resonance imaging or computerized tomography). Exclusion criteria for patients were as follows: visual hemi-neglect as determined by horizontal line bisection, copying of figures, and by means of the ''Bells test'' (Gauthier, Dehaut, & Joannette, 1989), evidence of cognitive decline, aphasia, apraxia, visual agnosia or physical impairment, cerebral tumor, multiple sclerosis, Alzheimer's disease, Parkinson's disease, and previous scanning training. The time span between the brain lesion and the examination date should comprise at least 6 months.

The research study was approved by the Institutional Review Board of the University of Tübingen (Germany) and was performed according to the Declaration of Helsinki. Following verbal and written explanation of the experimental protocol all subjects gave their written consent, with the option of withdrawing from the study at any time.

Of the 41 potential participants with hemianopia or quadrantanopia, two patients with unilateral neglect and seven patients with bi-hemispheric cerebral lesions leading to HVFDs in both hemifields were excluded. Two further patients withdrew after experiencing symptoms of motion sickness. Thirty eligible patients with HVFDs (20 with hemianopia and 10 with quadrantanopia) and 30 normal-sighted group-age-matched control subjects were finally enrolled into the study.

The etiology of the HVFD was in all cases a unilateral cerebrovascular lesion due to ischemia (21 patients), hemorrhage (one patient), rupture of intracerebral aneurysm (two patients), arteriovenous malformation (two patients) or hemorrhage after trauma (four patients). Time since lesion onset was at least 6 months (median: 20 months, range: 6 months to 18 years). There were 15 patients with right-hemispheric and 15 patients with left-hemispheric lesions, which were in the majority of cases located in the occipital lobe. The demographic characteristics of each of the 30 patients are listed in Appendix A.

2.2. Visual field assessment

Visual fields of patients were assessed with monocular threshold-related, slightly supraliminal automated static perimetry (sAS) within the central 30° visual field, binocular slightly supraliminal automated static perimetry (sAS) within the 90° visual field as well as binocular semi-automated 90° kinetic perimetry (SKP), each obtained with the OCTOPUS 101 Perimeter (Fa. HAAG-STREIT, Koeniz, Switzerland). Visual fields of control subjects were assessed with binocular slightly supraliminal automated static perimetry (sAS) within the 90° and binocular semi-automated 90° kinetic perimetry (SKP). Visual fields within the central 30° were performed with appropriate near correction. In the patient group – in accordance with a recent study of Wood et al. (2009) – homonymous visual field loss was classified as left vs. right and complete vs. incomplete. For patients with quadrantanopia, field loss was further classified as superior vs. inferior.

2.3. Experimental design

Performance in the collision avoidance task was assessed under VR-conditions. The VR environment was displayed on a cone-shaped projection screen. This screen provided a horizontal field of view of 150° and a vertical one of 70°. Subjects were seated upright with the back tightly on the chair and with their head in the axis of the conical screen. Eye level was set at 1.2 m altitude and distance to the screen at 1.62 m (Fig. 1).

The visual environment and the experimental procedures were programmed in the SGI OpenGL Performer™. The spatial resolution of the projected images was 2048 × 768 pixels displayed with a frame rate of 60 Hz.

2.4. Experimental task

The subject was instructed to ''drive'' along a straight road (Fig. 2A and B) and finally to drive through a virtual intersection with cross traffic without causing a collision.

The virtual driving distance to the intersection was 172.5 m and only straightforward movement of the virtual vehicle was possible. Subjects started each trial in a tunnel (Fig. 2A). After leaving the tunnel they could adjust their driving speed between 18 and 61.2 km/h (11.2–38 mph) by means of a joystick in order to avoid a collision with the cross traffic at the intersection. During the driving period it was not possible to stop the car. The subject should therefore estimate the time interval when the oncoming vehicle will arrive at the intersection. At the same time, the subject also needed to estimate the time interval that it will take for his/her vehicle to cross the road at the intersection (Matsumiya & Kaneko, 2008) and could adjust the speed in order to achieve the goal of preventing a collision. When subjects reached a white line 22.5 m before the intersection (Fig. 2B), they were not allowed to adjust their speed anymore. After this line they were automatically driven across the intersection with the last adjusted speed without further visual input. A potential collision was then calculated by the simulation program and was delivered to the examiner at the end of the experiment. Even in case of a collision, participants did not experience a virtual crash and did not receive any feedback about their performance, in order to maintain identical conditions for each trial.

All cars of the cross traffic had a constant speed of 50 km/h (31.1 mph) and on average there were equal numbers of vehicles from the left and right side. The experiment was programmed at two traffic density levels of ascending difficulty, which would generate collisions in 50% or 75% of the trials respectively – in case that a subject would begin the trial at a random position and would drive with random speed (i.e. chance level).

Subjects performed 30 trials: 15 trials for each density level in the same randomized order – and were free to perform head and eye movements. Prior to the start of the experiment all subjects underwent a training session lasting 5–10 min in order to understand the experimental demands and become familiar with the use of the equipment and the joystick. The experiment started after the participant reported that he/she has understood the task and has completed at least three ''collision-free'' trials at each of the two density levels. After each trial the simulation program recorded whether there was a collision or not. Participants were

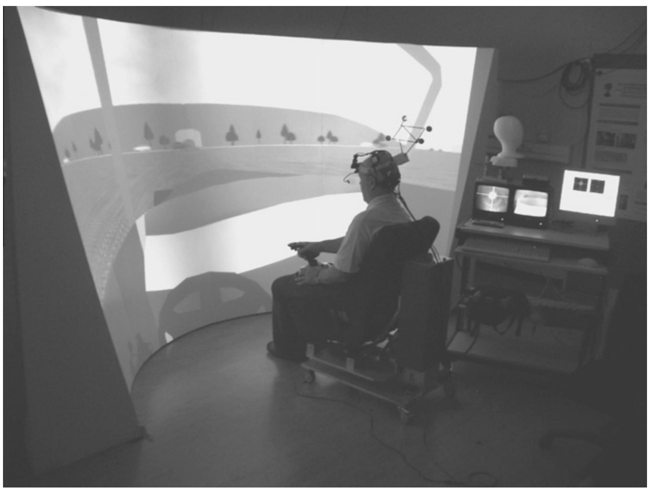

Fig. 1. Image of the experimental set-up. Study participant performing collision avoidance in front of the projection screen.

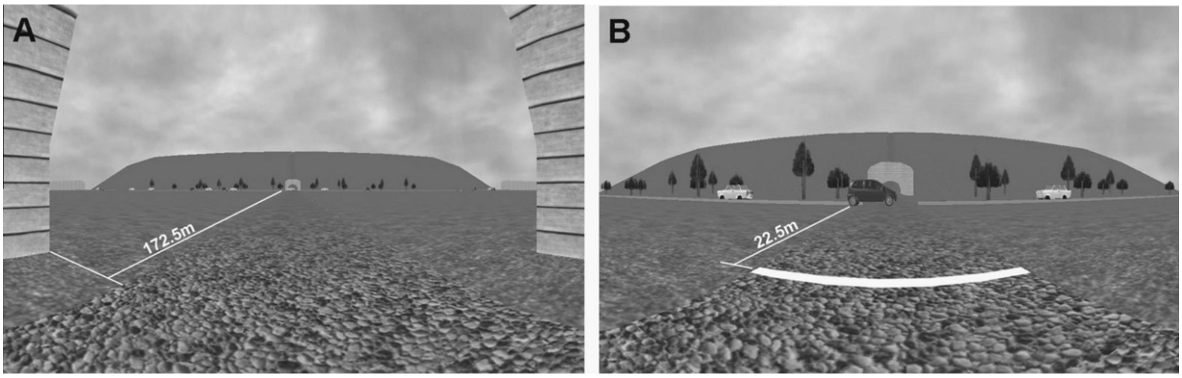

Fig. 2. (A) Start position of the virtual vehicle in the tunnel. The distance to the intersection (172.5 m) is depicted. (B) End position of the virtual drive at the white line 22.5 m before the intersection. The cross traffic at that moment is depicted (two cars driving from right to left and one car driving to the right).

not given feedback about their performance until the end of the experiment. Participants were encouraged to take breaks at will; testing resumed when the participant indicated they were ready. The time to complete the whole experiment ranged from 40 to 50 min.

2.5. Statistical methods

2.5.1. Visual field evaluation

From the binocular semi-automated 90° kinetic perimetry (SKP) we calculated the area of sparing within the affected hemifield (A-SPAR in deg^2) for the stimulus III 4e (background luminance 10 cd/m^2, angular velocity 3°/s, Fig. 3). Additionally, the area of sparing within the central 30° of the affected hemifield (A-30-SPAR) was also calculated (Fig. 3). This is the area most likely to be used during the collision avoidance task or when looking through the windshield of a car. An intact central 30° visual field is also recommended by the German ophthalmological society as a prerequisite for driving license. A software tool available on the OCTOPUS 101 Perimeter enables automatic calculation of the area within a specific isopter (in deg^2). In order to calculate the area of sparing for subjects with normal vision, they were arbitrarily assigned the right hemifield as the "affected" one, since any difference between the two hemifields in this case would be negligible. The A-30-SPAR was identical for all normal subjects. We used the binocular visual field, because it is assumed to provide more realistic information about the visual field a patient uses for performing daily activities (Schiefer et al., 2000).

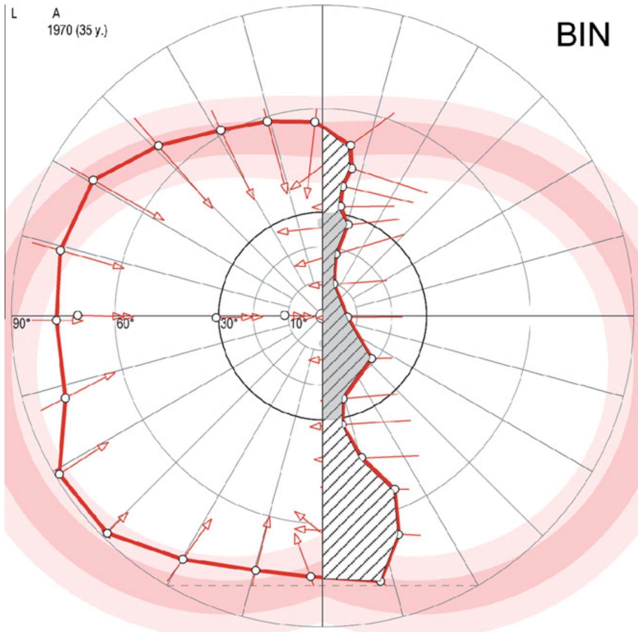

Fig. 3. Binocular visual field of a patient with a homonymous hemianopia to the right: Graphic representation of the area of sparing within the affected hemifield (A-SPAR as *hatched region*, obtained with stimulus III4e, angular velocity 3°/s) and the area of sparing within the central 30° of the affected hemifield (30-A-SPAR as *gray hatched region*).

2.5.2. Data analysis and statistics

Overall performance in the task was quantitatively assessed as the number of collisions for the 15 trials per density level. Data were analyzed using the statistical software JMP® (SAS Institute Inc., Cary, NC, USA) [www.jmp.com]. Since the number of collisions followed a Poisson distribution we applied a square root transformation in order to stabilize variances. We applied multifactorial analyses of variance with fixed factors group and traffic density and as random factor the individual nested under the factor group. The factor group refers to the division of participants in patients and normal subjects. Since the interaction terms between the fixed factors turned out to be non-significant, they were not included into the final models. The results are given as Hölder means together with the corresponding 95% confidence intervals. In our case the Hölder mean is the square of the arithmetic mean of the square roots of the observations.

In order to identify factors that might affect performance of patients, the effect of A-SPAR, age, gender, and traffic density on the number of collisions was investigated by means of fitting an analysis of covariance model stepwise by starting with the full model, setting the critical p-values at 5%, and eliminating all non-significant factors and their interactions. In order to stabilize the variances we took the square roots of the number of collisions. For Poisson distributed variables this results in a constant standard deviation of 0.5. The observed root mean square error was 0.54 which agrees well with the expected value. The final result of this stepwise procedure yielded a simple model, which contained all four main effects but without their interactions.

3. Results

3.1. Demographic data

The demographic summary statistics of patients and controls are given in Table 2. The ratio males/females for patients was 2.0 and for control subjects it was 1.5. There were no differences in age ($p = 0.79$, t-test) and gender ($p = 0.79$, Fisher's exact test) be-

Table 2
Demographic summary statistics (age and gender) of patients with HVFDs and control subjects.

	Hemianopia ($n_1 = 20$)	Quadrantanopia ($n_2 = 10$)	Combined ($N = 30$)	Controls ($N_o = 30$)
Age, mean (SD)	45.9 (16.4)	46.9 (16.1)	46.2 (16.0)	45.1 (15.4)
Gender, *N* (%)				
Female	5 (25)	5 (50)	10 (33)	12 (40)
Male	15 (75)	5 (50)	20 (67)	18 (60)
Side of lesion, *N* (%)				
Right	9 (45)	6 (60)	15 (50)	
Left	11 (55)	4 (40)	15 (50)	

tween patients and control subjects, reflecting group-matching with respect to age and gender. Additionally, a one-way ANOVA yielded no differences in regard to age ($F(2,57) = 0.079$, $p = 0.924$) between patients with right HH (45.3 ± 17 years, mean ± SD), patients with left HH (47.1 ± 15.5 years, mean ± SD) and control subjects (45.1 ± 15.4 years, mean ± SD).

3.2. Task performance analysis

The number of collisions of all subjects is shown in Fig. 4 separately for each traffic density level. Increasing the traffic density from 50% to 75% increases the mean number of accidents for controls by about 6 and for patients by about 7 ($p < 0.0001$, *F*-test). The difference between the controls and patients is about 1 for 50% density and 2 for 75% density ($p = 0.0061$, *F*-test).

Patients with hemianopia had significantly higher collision rates than controls in both traffic density levels, while there were neither significant differences in the collision rates of quadrantanopia patients compared with normal subjects nor with hemianopia patients (Fig. 5).

3.3. Side of collision

In order to compare the number of collisions between two hemifields within the same group, e.g. blind vs. seeing in patients, we used the matched pairs *t*-test. For comparisons between different groups we applied a one-way ANOVA. The data from four participants (three normally-sighted participants and one patient) with respect to the side of collision were not available due to spo-

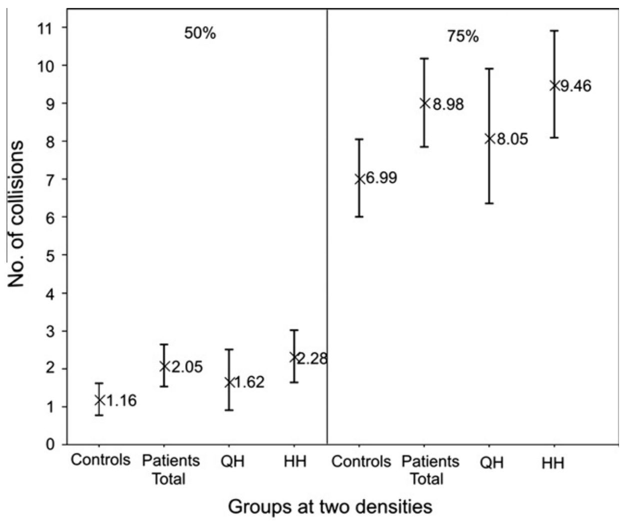

Fig. 5. Hölder mean number of collisions in controls, in the total patient group ("Patients total"), in patients with homonymous quadrantanopia (QH) and patients with homonymous hemianopia (HH) together with 95% confidence intervals. The means were estimated by a multifactorial analysis of variance with the fixed factors "group" (three levels) and "density" (two levels) and the random factor "individual", nested under the factor "group." The interaction between the two fixed factors was not significant ($p = 0.4546$) and was therefore ignored in the final model.

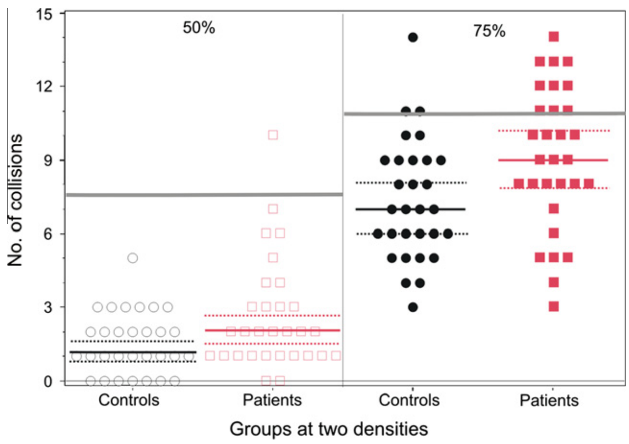

Fig. 4. Scatterplots of the number of virtual collisions at the 50% and 75% traffic density. The continuous black and red lines show the Hölder means and the dashed lines show the corresponding 95% confidence intervals. The red squares correspond to patients and the black circles refer to control subjects. The markers are open for density 50% and closed for density 75%. Increasing the traffic density from 50% to 75% increases the mean number of accidents for controls by about 6 and for patients by about 7 ($p < 0.0001$). The difference between the controls and patients is about 1 for 50% density and 2 for 75% density ($p = 0.0061$). The gray lines show the expected number of collisions in case that the subjects began the trials at a random time point and drove with random speed (i.e. with closed eyes): 7.5 collisions for 50% density and 11.25 collisions for 75% density. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

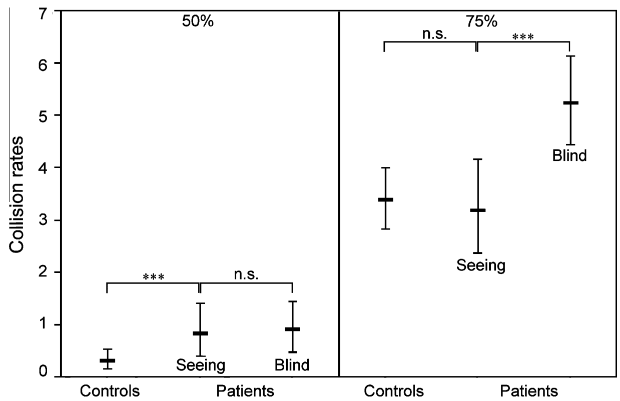

Fig. 6. Collision rates (number of collisions divided by the number of subjects at risk) together with their exact 95% CI based on the Poisson distribution in controls and patients for density 50% and 75%. Results of comparisons between groups (controls and patients) and between two hemifields within the same groups are shown. Due to missing data from four participants (three normally-sighted participants and one patient) with respect to the side of collision, analyses were carried out on 27 controls and 29 patients.

radic missing values in the recording process. While in the easier task (traffic density 50%) there were no differences in the number of collisions between patients' blind and seeing hemifield ($p = 0.821$), in density 75% patients collided more often with vehicles approaching from their blind side ($p = 0.002$). In terms of performance on patients' seeing side compared to normal subjects, in density 50% patients collided more often than normal subjects to their seeing hemifield ($p = 0.033$). However, in density 75% the number of collisions on patients' seeing side was similar to the number of collisions experienced by the normally-sighted ($p = 0.716$). These results are depicted graphically in Fig. 6.

3.4. Area of sparing

The effect of A-SPAR (area of sparing within the affected hemifield) and A-30-SPAR (area of sparing within the central 30° of the affected hemifield) on collision rate is presented in Fig. 7 as scatterplot of the number of collisions by A-SPAR and A-30-SPAR respectively. The slope of the curve for A-30-SPAR (−5/10,000 A-30-SPAR) was larger than the slope of the curve for A-SPAR (−0.6/10,000 A-SPAR), indicating a stronger negative correlation of A-30-SPAR with the number of collisions. However, this finding was expected, because the *Y*-axis values (number of collisions) are identical for both diagrams, while the *X*-axis values (A-SPAR or A-30-SPAR in deg^2) differ by almost one order of magnitude. Additionally, although the effect of both A-SPAR and A-30-SPAR were significant, there are large individual differences within our sample. It is noteworthy, that there are patients with almost identical A-SPAR or A-30-SPAR but considerably different collision rates. Furthermore, there are also some patients with even low A-SPAR or A-30-SPAR, who exhibit similar performance with that of normal-sighted control subjects.

3.5. Age and gender

The effect of age and gender on the total number of collisions is exhibited in Fig. 8. The data were modeled by square root transformed numbers of collisions. Backward stepwise regression anal-

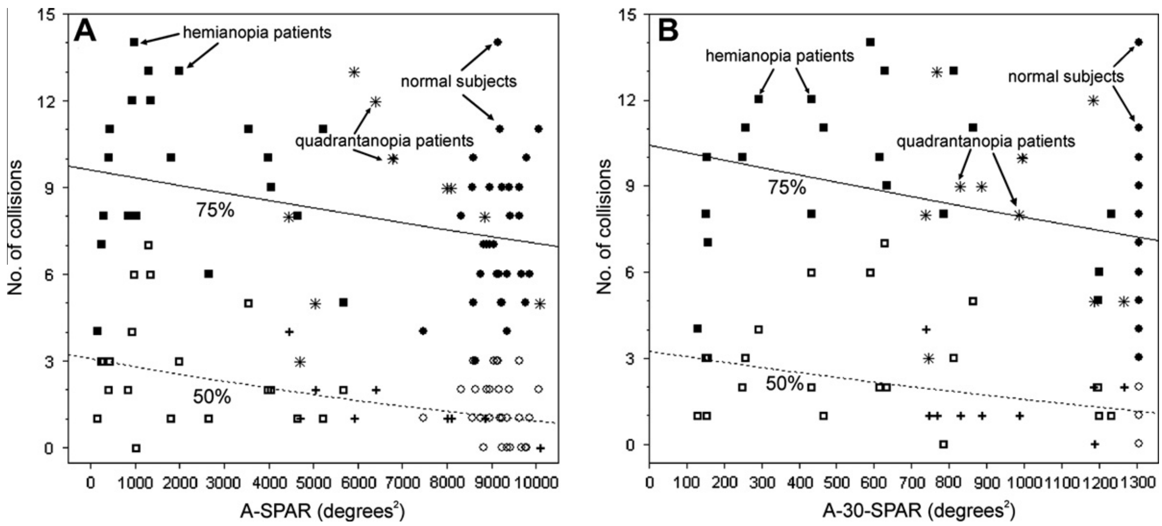

Fig. 7. Number of collisions by area of sparing (A: within the affected hemifield; B: within the central 30 deg^2 of the affected hemifield), data and regression curves for both traffic densities. The dots are labeled according to type and density. For 50% densities all labels are open and for 75% density they are filled. Normal subjects are shown by circles, hemianopia patients by squares and quadrantanopia patients by stars for 75% density vs. crosses for 50% density. (A) Because the intercepts differ for the two densities, the slopes of the linear component of the two curves are different though for the square roots the slopes are identical: −0.6/10,000 A-SPAR (95% CI −0.9 to −0.3/10,000 A-SPAR). (B) For the area of sparing within the central 30° of the affected hemifield (A-30-SPAR), the slope is −5/10,000 A-30-SPAR (95% CI −7/10,000 to −3/10000 A-30-SPAR).

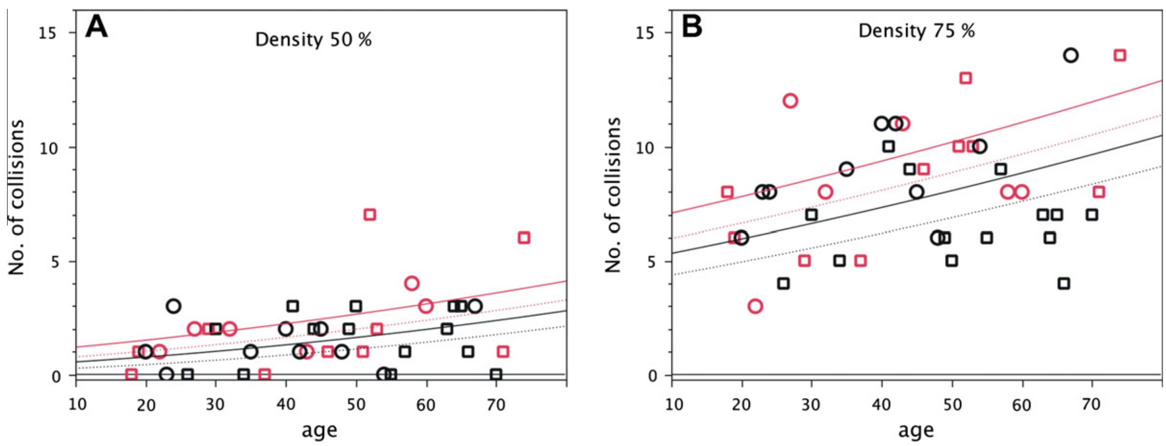

Fig. 8. The effect of age and gender on the number of collisions by traffic density in the total study population (A: density 50%; B: density 75%). Females are denoted by a circle and males by a square. The red markers (and lines) correspond to patients and the black markers (and lines) refer to control subjects. The continuous theoretical curves refer to females and the dashed lines to males. The number of collisions increases quadratically with age. Only the intercepts differ by gender, group and density for the square roots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

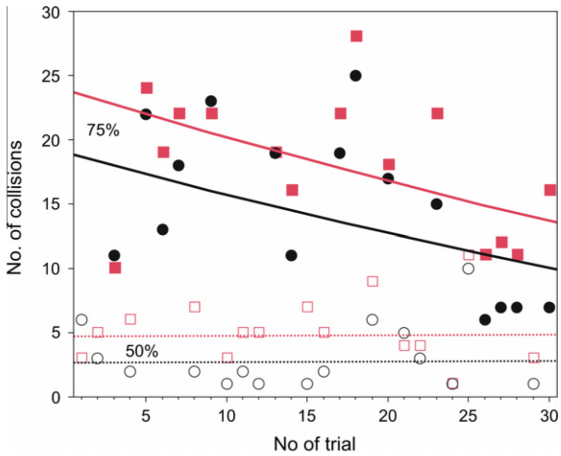

Fig. 9. A learning effect could only be seen at density 75% for patients and control subjects. The markers are the same as in Fig. 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ysis with fixed factors group (patient or normal), density (50% or 75%), gender and age, revealed non-significant interaction terms between them. All the main effects were significant: The number of collisions increases quadratically with age. The age effect is highly significant ($p = 0.0001$). The effects of group ($p = 0.0007$) and density ($p < 0.0001$) are discussed in Section 3.2. The gender effect is marginally significant ($p = 0.0456$). The age effect is not influenced by the other main factors (group, density and gender).

3.6. Brain lesion

Patients were divided into two subgroups by the median of their performance in both density levels using the median split method (Cohen, 2003): "performance above average" and "performance below average". Above average patients were compared with below average patients regarding the time span since brain lesion and side of brain lesion. Patients with performance above average did not differ from patients with performance below average regarding the side of brain lesion ($p = 1.00$, Fisher's exact test for dichotomous variables). Similarly, there was no difference in and time since brain lesion between patients with performance above average (3.49 ± 4.81 years, mean ± SD) and patients with performance below average (3.72 ± 4.57 years, mean ± SD) patients ($t(28) = -0.19$, $p = 0.85$, t-test for log transformed continuous variables). Data regarding the effect of brain lesion site on collision avoidance are reported elsewhere (Papageorgiou et al., 2011).

3.7. Learning effect

Performance of participants over time was investigated, in order to find out if participants decrease their collision rate over time. A learning effect was revealed for both patients and control subjects only in density 75%. The learning effect is exhibited in Fig. 9. The learning effect was not influenced by age and gender (data not shown).

4. Discussion

The goal of this study was twofold. First, it was designed to examine differences in performance between patients with HVFDs and normal-sighted control subjects in a collision avoidance task with moving obstacles. Second, we aimed to investigate the impact of the extent of the HVFD on collision avoidance, with the hypothesis that performance would not be solely explained by visual field-related parameters. Therefore we expected contribution of additional factors, e.g. age, gender, side of brain lesion and time span since lesion onset. We have examined a large homogenous patient group (regarding cause of HVFD) in comparison to an age-matched control group under standardized, repeatable VR-conditions.

4.1. Effect of HVFD

As hypothesized, subjects with HVFDs had on average more collisions than subjects with normal vision and in density 75% they experienced more collisions with vehicles approaching from the blind side than the seeing side. Additionally, in density 75%, the number of collisions on the seeing side of subjects with HVFDs was similar to the number of collisions experienced by normal subjects. In the easier task (density 50%) differences in collision rates between the blind and seeing hemifield were not obvious probably due to decreased visual and cognitive demands. These results suggest that patients with HVFDs are less efficient and experience difficulties in collision avoidance under VR-conditions, and are partly in accordance with a recent study of Bowers et al. (2009). They examined the effect of HH on detection of pedestrian figures within the controlled environment of a driving simulator. They concluded that detection rates of HH drivers for pedestrians on the blind side were significantly lower than detection rates for pedestrians on the seeing side and were significantly lower than those of drivers with normal vision. However, the experimental task in the study of Bowers et al. (2009) included detection of stationary pedestrians. Therefore the authors assumed that this may have resulted in lower detection rates than if the detection 'target' had been a moving car. In the present study, moving vehicles at an intersection were used in order to achieve more realistic circumstances in terms of collision avoidance. For this reason probably performance differences between patients and normal-sighted subjects were not as large in our sample as in the study of Bowers et al. (2009). Therefore, our results suggest that patients with HVFDs may achieve better ratings on collision avoidance tasks with moving obstacles than on detection of stationary targets at intersections. This may be related to the Riddoch phenomenon of statokinetic dissociation, whereby patients perceive moving but not static objects (Schiller et al., 2006). Statokinetic dissociation is often noted in recovering occipital lesions and has been commonly attributed to preserved islands of function within the occipital cortex. Variable degrees of dissociation of perception between moving and nonmoving stimuli have been also demonstrated in normal subjects and in patients with compression of the anterior visual pathways (Safran & Glaser, 1980). An additional explanation is provided by the division of the retino-cortical projection in two parallel pathways, the parvo- and the magno-cellular system (Nassi & Callaway, 2009). Magno-cellular neurons predominate in retinal periphery and are believed to mediate fast flicker and motion detection (Merigan, Byrne, & Maunsell, 1991; Merigan & Maunsell, 1990). Therefore, peripheral vision is much more sensitive to flicker perception than foveal vision, and this phenomenon might underlie our findings as well (Chapman, Hoag, & Giaschi, 2004; Schiller, Logothetis, & Charles, 1990).

Our findings cannot be directly contrasted to the results of Bowers et al. (2009), because the task requirements and the expected responses are different. In the study of Bowers et al. (2009) the subjects had to indicate detection of pedestrians by honking the car horn without any time constraints (i.e. even after they completed a turn at an intersection). At the same time they had to steer the virtual vehicle and operate all vehicle controls. We rather investigated subjects' ability to detect moving obstacles and avoid a collision in a strictly timely manner. Estimates of collision avoidance involve primarily perception of time-to-contact (Lee, 1976), i.e. the amount of time before a perceived object would reach the observer, the ability to detect the potential collision object and switch attention towards it, the ability to determine an appropriate avoidance response, and the ability to actually control the vehicle to avoid the collision under continuous demand on working memory (Horrey et al., 2007; Olson, 2002). Therefore, we did not offer the possibility of bringing the vehicle to a halt at the intersection. At most intersections without traffic lights, drivers would normally slow down on approach to the intersection and make a gap judgment either as they were slowing down (yield sign) or from a stationary position (stop sign). They would then choose an appropriate speed and time point at which to go through the intersection. While the inability to stop the vehicle might be a limitation in the study design, it was adopted in order to investigate how subjects perform in time-constrained collision avoidance situations and to quantify performance as the number of collisions by eliciting a "forced choice response."

One might argue against the choice of collisions as a measure of performance, because collisions are relatively infrequent events in real-world situations; however, intersections are challenging even for normal subjects (Bowers et al., 2009) and the available period to react, namely to perceive the size of the gap in terms of time to act (Simpson, Johnston, & Richardson, 2003), is not always unlimited – even in real world. In 2007, at least 22% of fatal accidents in the USA occurred at intersections (Fatality Analysis Reporting System Encyclopedia, 2007). Injury accidents at intersections account for 41.2% in Germany, which is quite close to the European median (43%), and 50.1% in the UK. This is due mainly to the fact that accident scenarios at intersections are among the most complex ones and different categories of road users interact in these limited areas with crossing trajectories (Cooperative Intersection Safety, 2009).

The presence and extent of the HVFD, expressed as a lower area of sparing in the affected hemifield (A-SPAR) or in the central 30° of the affected hemifield (A-30-SPAR), is associated with worse performance in the present collision avoidance task. This is additionally illustrated by the finding that patients with hemianopia displayed worse performance than those with quadrantanopia (Fig. 5). The negative correlation of A-30-SPAR with the number of collisions was stronger than that of A-SPAR, indicating that the central visual field is more relevant for collision avoidance under VR-conditions. This finding is in agreement with recent European standards for the visual field of drivers, stating that no defects should be present within the central 20° for holders of ordinary driving license, or within the central 30° for heavy goods vehicle and public service vehicle licence holders (Changes to Annex II of the 2nd EC Directive on Vision and Driving, 2011). These field values are based on the observation that this area is of particular importance for visual perception during driving (Schiefer et al., 2000). However, the weak relationship between A-SPAR or A-30-SPAR and the number of collisions, as shown by the slope of the regression curves (Fig. 7), suggests that perimetric findings per se are inadequate in predicting collision avoidance among patients with HVFDs under VR-conditions. Few studies have assessed the impact of the extent of the HVFD on performance by using different performance measures and study designs. Hence, comparing our results with previous findings may only provide indicative data. In agreement with Racette and Casson (2005) we concluded that hemianopia tended to have a worse impact on driving performance than quadrantanopia, while quadrantanopic drivers did not differ in their performance from normal-sighted subjects (Fig. 5). Furthermore, in the present study 23 out of 30 patients with HVFDs (76.7%) performed within the range of normal subjects in both difficulty levels, if the outlier normal subject with excessively high collision rates is excluded (Fig. 4). These findings are consistent with a recent on-road study (Wood et al., 2009), where 88% of quadrantanopic patients and 73% of patients with HVFDs received safe ratings (Wood et al., 2009). On the other hand, our results appear to be at odds with the on-road studies of Tant et al. (2002) and Kooijman et al. (2004), because in these studies subjects had been referred due to suspected driving safety concerns.

4.2. Variability among patients with HVFDs and among various studies

The predictive power of A-SPAR is additionally limited by the fact that large individual variability occurs (Fig. 6). A high degree of between-subject variability in patients with HVFDs in VR or on-road driving tasks has been reported in other studies as well, and may reflect aging processes (see Section 4.3), individual compensation capacity and working memory availability (Bowers et al., 2009; Hardiess et al., 2010; Lövsund, Hedin, & Törnros, 1991; Racette & Casson, 2005; Wood et al., 2009). Other factors that may account for the great variability in the performance of patients with HVFDs among studies are the differences in the experimental design (naturalistic tasks, virtual reality or on-road driving assessments) and the performance measures, the presence of a normal-sighted control group, the reason for participation in the study, the sample sizes and the inclusion criteria of subjects – i.e. time after lesion onset, presence of hemi-neglect (Table 1). We have tried to minimize these limitations, since our subject group was relatively large, homogenous in regard to the etiology of the HVFD and free of selection bias, there were no safety concerns and our study did not include a driving test, but an assessment of performance in a cognitively challenging task under repeatable VR-conditions. However, the observed variability highlights the need for development of a standardized, functional task which could also be used as an outcome measure in rehabilitation training programs (Bowers, Keeney, & Peli, 2008; Szlyk et al., 2005).

4.3. Age effect

Increasing age in the present collision avoidance task was associated with decreasing performance. Previous studies have reported deterioration in simulated tasks or on-road assessments with increasing age (Lövsund, Hedin, & Törnros, 1991; Szlyk, Brigell, & Seiple, 1993; Wood, 2002). However, there is little work investigating how age affects performance in time-constrained collision-avoidance situations. Bowers et al. (2009) found that older HH drivers had lower pedestrian detection rates than younger HH drivers, indicating a reduction in the ability to compensate for the field loss with increasing age. Szlyk, Brigell, and Seiple (1993) also suggested that age-related losses, when compounded by stroke-associated impairments, significantly influenced visuospatial driving-related skills. A recent study suggested that collision avoidance situations are increasingly difficult with advancing age and older adults are less efficient at perceiving an affordable gap when spatiotemporal relations are of importance (Lobjois et al., 2008). Our findings confirm these results and extend the age effect in collision avoidance tasks for patients with HVFDs as well. Interestingly, there was no interaction of age and the presence of HVFDs, thus indicating a similar (highly significant) age effect in both patients and normal-sighted subjects. Age-related changes, like a decline in cognitive abilities, a slowing down of information processing or even a deterioration of exploration ability, may probably affect object detection and subsequent reaction ability in such interactive scenarios (Ryan, Legge, & Rosman, 1998).

4.4. Learning effect

During the short-term exposure to the more challenging conditions of higher traffic density, both visually-impaired and normally-sighted participants had similar learning curves, which should be attributed to task learning.

4.5. Brain lesion

Consistent with previous findings (Bowers et al., 2009), we did not find any differences in the time span since the brain lesion between patients with "performance above average" and "performance below average". The reason is probably that our patient group was homogenous regarding cause of the brain lesion, and the time span after lesion onset was at least 6 months. Recent studies suggest that 6 months postinjury is the time span after which spontaneous recovery of visual field is unusual following vascular lesions, when patients have adapted a different compensatory eye movement strategy (Pambakian et al., 2004; Zhang et al., 2006).

Concerning the side of the brain damage, one might expect that patients with right-hemispheric lesions would perform worse, presumably because of a higher incidence of visuo-spatial deficits like neglect (Korner-Bitensky et al., 2000; Meerwaldt & Van Harskamp, 1982). However, no differences in performance were revealed between patients with left- and right-hemispheric lesions in agreement with earlier studies (Bowers et al., 2009; Szlyk, Brigell, & Seiple, 1993; Wood et al., 2009; Zihl, 1995). This may be due to the fact that patients with clinical evidence of neglect or signs of impaired lateralized attention in the paper-and-pencil tests were excluded from the present study. Another possible explanation is that both hemispheres play equivalent roles in the spatial guidance of visual searching (Ratcliff & Newcombe, 1973; Zihl, 1995).

5. Conclusion

Our results for patients with HVFDs seem to extend the findings of a recent study on impaired detection of stationary objects (Bowers et al., 2009), to impaired collision avoidance of moving obstacles at intersections as well. However, the extent of HVFDs is weakly associated with performance in the present collision avoidance task under VR-conditions. Performance of some patients is similar to that of normal subjects, which may be attributed to the development of compensatory viewing behavior (Hardiess et al., 2010; Wood et al., 2011). Due to this wide between-subject variability, generalization of the findings regarding the impact of HVFDs is misleading and individualized approaches of compensatory functional behavior of patients with HVFDs are necessary. In future studies we will attempt to find predictors of visual compensation in realistic tasks and measure not only the extent of the visual field defect, but also the extent to which impaired individuals adopt compensatory viewing strategies. Assessment of visual exploration (head and eye movements), functioning in everyday life and multimodal approaches (performance in different tasks) may play an important role in determining the visual capacities of patients with homonymous field loss (Hardiess et al., 2010; Wood et al., 2011).

Disclosure

Ulrich Schiefer is consultant of HAAG-STREIT, Inc., Koeniz, Switzerland, he holds patents, related to the semi-automated kinetic perimetry.

Acknowledgments

The authors are thankful to Mrs. Simone Bahlo (Bad Urach Rehabilitation Center) for assisting with the recruitment of patients and to Dr. William Hart for editing the final version of the manuscript. This work was supported by the following grants: European Union (PERACT-Marie Curie Early Stage Research Training, MEST-CT-2004-504321), Deutsche Forschungsgemeinschaft (SFB 550-A4), GRK 778.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2011.10.019.

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Vision Research 65 (2012) 25–37

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Gaze patterns predicting successful collision avoidance in patients with homonymous visual field defects

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ARTICLE INFO

Article history:
Received 8 November 2011
Received in revised form 23 May 2012
Available online 18 June 2012

Keywords:
Homonymous visual field defects
Collision avoidance
Virtual reality
Gaze
Compensation
Working memory

ABSTRACT

Aim of the present study was to identify efficient compensatory gaze patterns applied by patients with homonymous visual field defects (HVFDs) under virtual reality (VR) conditions in a dynamic collision avoidance task. Thirty patients with HVFDs due to vascular brain lesions and 30 normal subjects performed a collision avoidance task with moving objects at an intersection under two difficulty levels. Based on their performance (i.e. the number of collisions), patients were assigned to either an "adequate" ($HVFD_A$) or "inadequate" ($HVFD_I$) subgroup by the median split method. Eye and head tracking data were available for 14 patients and 19 normal subjects. Saccades, fixations, mean number of gaze shifts, scanpath length and the mean gaze eccentricity, were compared between $HVFD_A$, $HVFD_I$ patients and normal subjects. For both difficulty levels, the gaze patterns of $HVFD_A$ patients ($N = 5$) compared to $HVFD_I$ patients ($N = 9$) were characterized by longer saccadic amplitudes towards both the affected and the intact side, larger mean gaze eccentricity, more gaze shifts, longer scanpaths and more fixations on vehicles but fewer fixations on the intersection. Both patient groups displayed more fixations in the affected compared to the intact hemifield. Fixation number, fixation duration, scanpath length, and number of gaze shifts were similar between $HVFD_A$ patients and normal subjects. Patients with HVFDs who adapt successfully to their visual deficit, display distinct gaze patterns characterized by increased exploratory eye and head movements, particularly towards moving objects of interest on their blind side. In the context of a dynamic environment, efficient compensation in patients with HVFDs is possible by means of gaze scanning. This strategy allows continuous update of the moving objects' spatial location and selection of the task-relevant ones, which will be represented in visual working memory.

1. Introduction

Homonymous visual field defects (HVFDs) represent the most frequent type of visual deficits after acquired brain injury (Zihl, 1999), affecting nearly 80% of patients with unilateral postchiasmal brain damage (Zihl, 1995). Sufficient spontaneous recovery of the visual field is seldom and may occur within the first 6 months (Zhang et al., 2006). In the majority of patients, HVFDs are chronic manifestations that create a marked amount of subjective inconvenience in everyday life (Gall et al., 2009; Papageorgiou et al., 2007). Patients typically complain about difficulties with reading (i.e. hemianopic dyslexia) and visual exploration (Hardiess et al., 2010; Schuett et al., 2008; Zihl, 2000). The visual exploration impairment is characterized by the disability to gain a quick overview of the visual scene especially in unfamiliar surroundings or complex situations (Mort & Kennard, 2003; Zihl, 1995). Impaired visual exploration is associated with longer visual search times, shorter saccades, numerous refixations, target omissions, and longer, unsystematic scanpaths (Hardiess et al., 2010; Mort & Kennard, 2003; Pambakian et al., 2000; Tant, Cornelissen, Kooijman, & Brouwer, 2002b; Zihl, 1995).

Driving has been also considered to be problematic for patients with HVFDs. The majority of on-road studies and simulator experiments have highlighted poor steering control, incorrect lane position and difficulty in gap judgment as the primary problems of drivers with HVFDs (Bowers, Mandel, Goldstein, & Peli, 2009; Bowers, Mandel, Goldstein, & Peli, 2010; Szlyk, Brigell, & Seipel, 1993; Tant et al., 2002b; Wood et al., 2009). Additionally, in a recent study investigating self-reported driving difficulty, drivers with hemianopic and quadrantanopic field loss expressed significantly more difficulty with driving maneuvers involving peripheral vision and independent mobility, compared to those with normal visual fields (Parker et al., 2011).

However, driving performance of some patients is similar to that of normal subjects, while others display obvious vehicle control problems (Papageorgiou et al., 2012; Parker et al., 2011;

Abbreviations: HVFD, homonymous visual field defect; VR, virtual reality.

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http://dx.doi.org/10.1016/j.visres.2012.06.004

Tant et al., 2002b; Szlyk et al., 1993; Wood et al., 2009). This variation might be attributed to the fact that some patients develop adaptive eye- and head-movements allowing them to efficiently compensate for the visual field loss. Further evidence for the hemianopic compensatory viewing behavior is available from naturalistic experiments. When viewing simple patterns patients with HVFDs spend most of their time looking toward their blind hemifield in order to bring more of the visual scene into their seeing hemifield (Ishiai, Furukawa, & Tsukagoshi, 1987). This deviation of the fixation point towards the hemianopic side was considered to be an efficient compensatory strategy and has since been observed in numerous other tasks, including dot-counting (Hardiess et al., 2010; Tant et al., 2002b; Zihl, 1995), viewing of natural and degraded images (Pambakian et al., 2000) and comparative visual search (Hardiess et al., 2010).

To date, hemianopic gaze patterns have been assessed with tasks on stationary displays, usually limiting the field of view to a computer screen. Although the most demanding tasks for hemianopic patients arise within dynamic – commonly time-constrained – situations in our constantly changing visual world (Zihl, 1995), little is known about the exploration strategy applied by those patients when confronted with moving stimuli. Recent evidence suggests that efficient oculomotor adaptation to visual field loss is highly specific and task-dependent (Hardiess et al., 2010; Schuett et al., 2009), therefore specialized approaches seem necessary in order to assess visual behavior of hemianopic patients towards dynamic objects in contrast to stationary targets. Some clues to visual behavior of hemianopes in dynamic, naturalistic environments have been provided by on-road experiments; however, the use of accurate eye and head tracking systems under such scenarios is still not established (Wood et al., 2011).

Moreover, most of the previous studies assessed hemianopic patients as a group in contrast to normal subjects. Given that some of the patients compensate for their visual deficit, it might be more appropriate to identify these patients according to functional performance measures, and study their gaze patterns in comparison to patients with inadequate compensation and normal subjects as well (Hardiess et al., 2010; Wood et al., 2011; Zihl, 1999). Therefore, the aim of the present study was to identify efficient compensatory gaze patterns applied by patients with HVFDs in a collision avoidance task with moving stimuli under virtual reality (VR) conditions. We hypothesized that patients with high success rates in completing the task will demonstrate compensatory scanning patterns, characterized by increased gaze movements especially towards moving objects of interest on their blind side and that this gaze strategy will be more evident in the more difficult task.

2. Material and methods

2.1. Participants

Thirty eligible patients with HVFDs (20 with hemianopia and 10 with quadrantanopia) and 30 normal-sighted group-age-matched control subjects were enrolled in the study. All participants were at least 18 years old, had best corrected monocular (near and distant) visual acuity of at least 20/25 and normal function and morphology of the anterior visual pathways as evaluated by ophthalmological tests (fundus and slit-lamp examinations, ocular alignment, ocular motility). The group-age-matched control subjects additionally showed normal visual fields and no history of brain injury, physical or cognitive impairment. Patients had a homonymous visual field defect, varying from complete homonymous hemianopia to homonymous paracentral scotomas, due to a unilateral vascular brain lesion, which was documented by neuroradiological findings (magnetic resonance imaging or computerized tomography). The time span between the brain lesion and the examination date comprised at least 6 months. Exclusion criteria for patients were as follows: visual hemi-neglect as determined by horizontal line bisection, copying of figures, and by means of the "Bells test" (Gauthier, Dehaut, & Joannette, 1989), evidence of cognitive decline, aphasia, apraxia, visual agnosia or physical impairment, cerebral tumor, multiple sclerosis, Alzheimer's disease, Parkinson's disease, and previous scanning training. The demographic data of patients are presented in Appendix 1. The research study was approved by the Institutional Review Board of the University of Tübingen and was performed according to the Declaration of Helsinki. Following verbal and written explanation of the experimental protocol all subjects gave their written consent, with the option of withdrawing from the study at any time.

2.2. Virtual reality environment

The VR environment was displayed on a large cone-shaped projection screen (horizontal field of view: 150°, vertical: 70°) allowing for natural viewing behavior (Hardiess, Gillner, & Mallot, 2008; Hardiess et al., 2010). Subjects were seated upright with the back tightly on the chair and with their head in the axis of the conical screen (eye level: 1.2 m altitude, distance to the screen: 1.62 m). The virtual environment and the experimental procedures were programmed in C++ using the SGI OpenGL Performer™ (spatial resolution of the generated images: 2048 by 768 pixels). To illuminate the whole projection screen, two video projectors each with 1024 by 768 pixel resolution and a fixed 60 Hz frame rate were used. The light in the experimental lab was dimmed nearly to complete darkness in order to avoid disturbing cues from the surround.

Eye-in-head movement recordings were realized with an infrared light based, head mounted and lightweight eye tracker (bright pupil type, model 501 from Applied Science Laboratories, Bedford, USA). The tracker uses the pupil-corneal-reflection method and enables an accuracy two degrees or better, depending on the eccentricity of the eye position. Real time delay was 50 ms. To record head-in-space movements, an infrared light based tracker system (ARTtrack/DTrack from ART GmbH, Weilheim, Germany) with 6 degrees of freedom, 0.1° accuracy, and a real time delay of 40 ms was used. A configuration of four light reflecting balls fixed to the eye tracker device and thus to the head provided the tracking target for the head tracking system. Both trackers had a fixed temporal sampling frequency of 60 Hz. The online position recordings from eyes and head were transmitted via socket connection to an experimental PC for storage.

We used a nine-point grid for equipment calibration which was carried out at the beginning of the experiment. Subjects started each trial in a tunnel. Prior to each trial, patients initially fixated a central cross for 5 s to ensure that their gaze commenced at the center of the projection screen (point of origin). All gaze (eye and head) measurements are reported relative to this point of origin. After leaving the tunnel the participants could adjust their driving speed between 18 and 61.2 km/h (11.2–38 mph) by means of a joystick in order to avoid a collision with the cross traffic at the intersection. During the driving period it was not possible to stop the car. The subjects were instructed to "drive" along a straight road (Fig. 1a and b) and finally to cross a virtual intersection without causing a collision. A lateralization effect has been suggested for patients with HVFDs in terms of failing to detect stationary objects in the hemianopic side (Bowers et al., 2009). Therefore, we used an intersection with cross traffic in order to elicit visual scanning by eye and head movements and detect participants' potential to compensate. The driving distance to the intersection was 172.5 m and the only possible movement of the virtual vehicle was straight ahead. When subjects reached a white line 22.5 m before the intersection (Fig. 1b), they were automatically driven across the intersection with the last adjusted speed without further visual input. A potential collision was

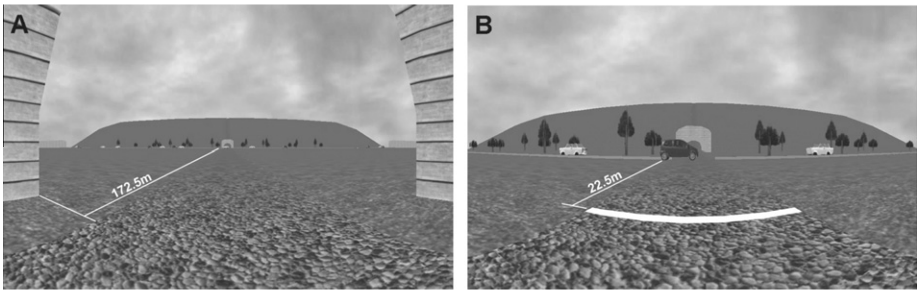

Fig. 1. Start (−172.5 m) and end (−22.5 m) positions of the virtual drive. (a) Start position of the virtual vehicle in the tunnel. The distance to the intersection is also depicted. (b) End position of the virtual drive at the white line 22.5 m before the intersection.

then calculated by the simulation program and was delivered to the examiner at the end of the experiment. Even in case of a collision the participants did not experience a virtual crash and did not receive any feedback about the result during the experiment, in order to maintain identical conditions for each trial. All vehicles of the cross traffic had a constant speed of 50 km/h (31.1 mph), were either red Renault Twingo or white Trabant vehicles (Fig. 1b) with equal numbers of vehicles approaching from the left and right side. The experiment was programmed at two traffic density levels of ascending difficulty, which would generate collisions in 50% or 75% of the trials respectively – in case that a subject would begin the trial at a random position and would drive with random speed (i.e. chance level). Subjects performed 30 trials in the same randomized order (i.e. 15 trials for each density level) and were free to perform head and eye movements. Prior to the start of the experiment all subjects underwent a training session lasting 5–10 min. The time to complete the whole experiment ranged from 40 to 50 min.

2.3. Visual field assessment

Visual fields of patients were assessed with monocular threshold-related, slightly supraliminal automated static perimetry (sAS) within the central 30° visual field, binocular slightly supraliminal automated static perimetry (sAS) within the 90° visual field as well as binocular semi-automated 90° kinetic perimetry (SKP), each obtained with the OCTOPUS 101 Perimeter (Fa. HAAG-STREIT, Koeniz, Switzerland). Visual fields of control subjects were assessed with binocular slightly supraliminal automated static perimetry (sAS) within the 90° and binocular semi-automated 90° kinetic perimetry (SKP).

2.4. Data analysis and statistics

The MATLAB software (MathWorks Company, Natick, USA) was used to analyze the recorded head and eye tracking data. The gaze vector was calculated as resultant of the head and eye vectors. Thus, the gaze vector combines both the head-in-space and the eye-in-head vectors. Fixations were defined as sections of the gaze trajectory where gaze velocity did not exceed 100°/s for at least 120 ms. A gliding window procedure was used to distinguish such gaze fixations (stable gaze position related to the processed stimulus region) from gaze saccades (Hardiess, Gillner, & Mallot, 2008). Since gaze position was calculated from the sum of eye-in-head plus head-in-space positions, the terms "saccades" and "fixations" used in the text refer to gaze saccades and gaze fixations respectively.

Statistical analysis was conducted using the statistical software JMP® (SAS Institute Inc., Cary, NC, USA) [www.jmp.com]. Task performance was quantitatively assessed as the number of collisions for the 15 trials per density level. A distinction between "adequate" ($HVFD_A$) and "inadequate" ($HVFD_I$) patients was based on their task performance (i.e. number of collisions) in both difficulty levels by means of the median split method (Altgassen et al., 2007; Cohen, 2003; Hardiess et al., 2010; Machner et al., 2009; Zihl, 1999). The square roots of the number of collisions for each density level were used to span a two-dimensional co-ordinate system, where each point represents a patient (Fig. 2). The square root transformation of the data was used in order to stabilize the variance for Poisson distributed variables. This method implements an intrinsic functional criterion, which is based on the experimental results. Additionally, the median split introduces a joined performance measure for the two tasks of varying difficulty and divides patients into two subgroups ($HVFD_A$ and $HVFD_I$) each one consisting of 15 patients.

For the assessment of visual exploration we calculated the following gaze-related parameters: total number of fixations, mean duration of fixations (ms), percentage of fixations on vehicles (%), percentage of "straight-ahead" fixations (i.e. fixations on the intersection, %), scanpath length (i.e. the sum of all saccadic amplitudes) and number of gaze shifts (i.e. gaze transitions between left and right hemifield). Finally, we calculated the "mean gaze eccentricity" (°), as the average distance of gaze position from the intersection. In addition, we performed hemispace and directional analyses (Tant et al., 2002b; Zihl, 1995). The hemifield is defined in terms of

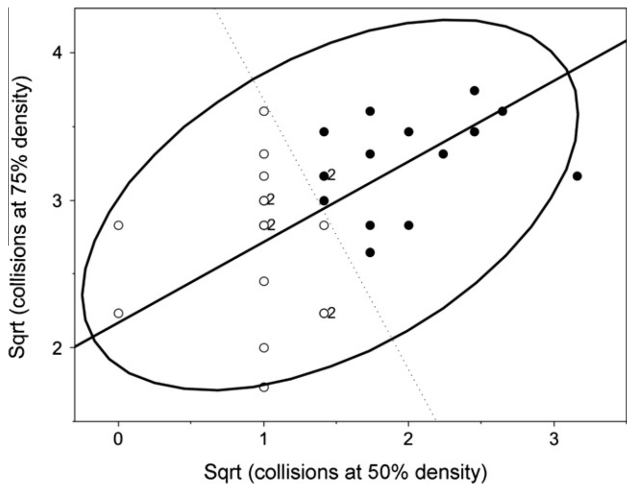

Fig. 2. Median split method. The square roots of the number of collisions for the density levels 50% (*x* axis) and 75% (*y* axis) were used to span a two-dimensional co-ordinate system, where each point represents a patient. The ellipse contains 95% of the bivariate normal distribution. The continuous line is the principal axis of the ellipse. Based on its slope, the formula for the weighted sum "wsum" is calculated from both square roots: 1.83 × sqrt(collisions at 50%) + sqrt(collisions at 75%). The median is 5.55. Patients with wsum > median are shown as black dots and were denoted as "inadequate" (i.e. more collisions or $HVFD_I$), while all remaining patients (with wsum < median) are shown as white dots and were denoted as "adequate" (i.e. fewer collisions or $HVFD_A$). The label "2" on some positions indicates coinciding values. The correlation between patients' performance at 50% and 75% density was significant (Rho-S = 0.51, $p < 0.05$).

the vertical center of the screen (Tant et al., 2002b), as left/right for normally-sighted subjects and blind/seeing for patients. Hemispace analysis was performed on the proportion (%) of gaze eccentricity to the blind or left hemifield and the proportion of fixations landing at each hemifield. Proportion of gaze eccentricity to the blind or left hemifield was calculated as following: (mean gaze eccentricity to the blind or left hemifield $\times$ 100)/(mean gaze eccentricity to the blind or left hemifield + mean gaze eccentricity to the seeing or right hemifield). Directional analysis was performed on the mean saccadic amplitude (°). In accordance with an earlier study (Zihl, 1995), the terms "visual exploration", "visual searching" and "visual scanning" are used synonymously.

In order to identify gaze patterns associated with successful collision avoidance, the above gaze-related parameters were compared across the three participant groups (adequate patients $HVFD_A$, inadequate patients $HVFD_I$ and normal subjects N) by one-way ANOVA. Subsequent post hoc comparisons were performed using the Tukey's HSD test. In order to test for hemispace preferences, unpaired *t*-tests were conducted between hemifields (left and right for normal subjects, blind and seeing for patients). Matched pairs *t*-tests were performed between the levels of "traffic density" (50% and 75%), in order to investigate the influence of task difficulty. As multiple tests were carried out, the significance level was adjusted using a Bonferroni correction to an alpha-level of 0.05 for multiple comparisons. All data sets were tested for normality by the Shapiro–Wilk test; for non-normally distributed data, the Kruskal–Wallis test for multiple comparisons and the Mann–Whitney U test were used.

3. Results

3.1. Demographic data

Thirty patients with HVFDs (20 patients with homonymous hemianopia, 10 patients with homonymous quadrantanopia) with a mean age of 46.2 ± 16 years and 30 normal subjects with a mean age of 45.1 ± 15.4 years were included in the study. Mean time since lesion onset was 2.7 years and exceeded 1 year in the vast majority of cases (26 out of 30 patients). There were 15 patients with right-hemispheric and 15 patients with left-hemispheric lesions. There were no differences in age ($p = 0.79$, *t*-test) and gender ($p = 0.79$, Fisher's exact test) between patients and control subjects, reflecting group-matching with respect to age and gender.

Nineteen out of 30 patients reported that they were regularly driving in the past but ceased driving at the time of the brain injury, eight out of 30 patients reported regularly driving both in the past and currently, and three patients were lifetime nondrivers (aged 18, 19 and 21 years, see Appendix 1). All 30 normal subjects reported regularly driving in the past and currently. There were no differences regarding years of driving experience between patients (22.4 ± 11.7 years, range: 5–45 years) and normal subjects (19.9 ± 11.1 years, range: 2–35 years) ($p = 0.42$, *t*-test).

3.2. Task performance: number of collisions and trial duration

According to the median split method, patients were divided into two subgroups by the median of their performance (number of collisions) in both density levels: 15 "adequate" ($HVFD_A$) and 15 "inadequate" ($HVFD_I$) patients (Fig. 2). A significant correlation was shown between patients' performance at 50% and 75% density (Rho-S = 0.51, $p < 0.05$). Normal subjects and $HVFD_A$ patients had similar collision numbers, while $HVFD_I$ patients showed significantly more collisions than the other participant groups at both traffic densities (Fig. 3). In addition, trial duration, i.e. the time needed to complete the task, was similar between normal subjects and $HVFD_A$ patients, while $HVFD_I$ patients showed shorter trial duration than normal subjects (Fig. 3).

3.3. Comparison of gaze-related parameters between normal subjects, $HVFD_A$, and $HVFD_I$ patients

Regarding analysis of gaze-related parameters, 14 patients (five $HVFD_A$ and nine $HVFD_I$) and 19 normal subjects (N) were evaluable, because 27 participants with insufficient eye and head tracking data had to be excluded (16 patients and 11 normal subjects). The relatively high rate of missing gaze tracking data represents a limitation of our study and is due to the wide range of possible gaze positions allowed on the large projection screen (horizontal view 150°). Gaze tracking errors occur when either the corneal reflection or the pupil moves out of the range of the eye camera, i.e. in case of saccadic movements to peripheral stimuli. The off axis movements are often brief and, therefore, not fully followed by a head movement to re-center the eye within the tracking range (Reimer & Sodhi, 2006). Such eye movements to peripheral targets were common in our study, because we aimed to assess scanning behavior over a large area of the visual field. That was the reason for using a wide projection screen and an appropriate intersection task. Additionally, the use of a high cutoff rate (of 5%) for accepting

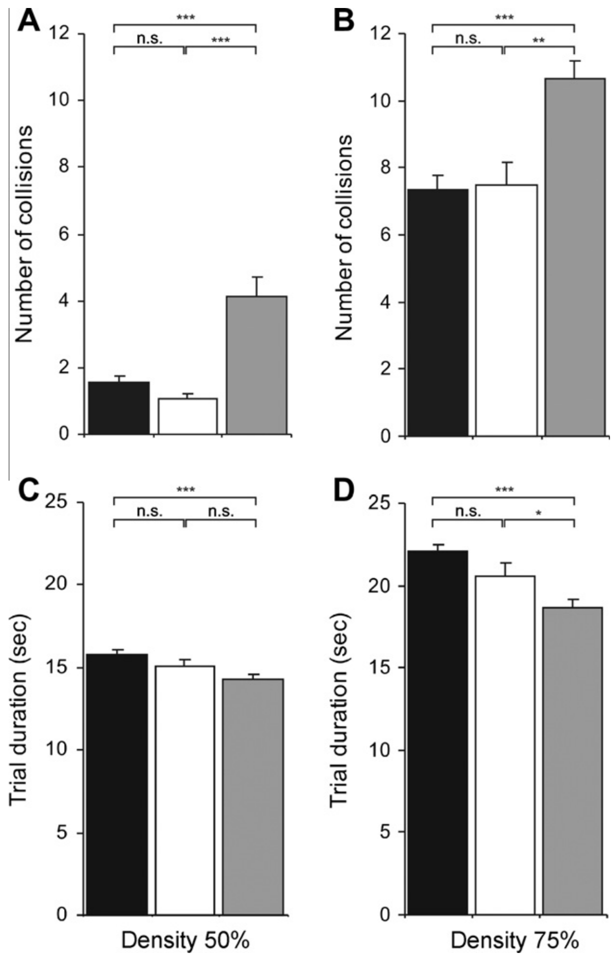

Fig. 3. Number of collisions for traffic density 50% (A) and 75% (B), and mean trial duration for traffic density 50% (C) and 75% (D). Comparisons were performed between normal subjects (black bars), adequate-$HVFD_A$ patients (white bars) and inadequate-$HVFD_I$ patients (grey bars). Tukey's post hoc test was conducted in order to detect significant differences between groups ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons). Error bars indicate standard error of the mean (sem).

usable data, the technical characteristics of the tracking equipment (limited tracking area) and the fact that participants "preferred" eye movements without accompanying head movements resulted in the high rate of missing gaze data.

There were no differences between the two patient subgroups ($HVFD_A$ and $HVFD_I$) regarding age ($p = 0.65$, *t*-test), the time span since brain lesion ($p = 0.69$, Mann–Whitney U test) and the degree of macular sparing ($p = 0.35$, Mann–Whitney U test). Research has suggested that novice drivers have different search strategies compared with experienced drivers (Chapman & Underwood, 1998; Mourant & Rockwell, 1972). In this study population there was no difference between normal subjects, $HVFD_A$ and $HVFD_I$ patients regarding years of driving experience ($p = 0.67$, Kruskal–Wallis test).

In order to identify gaze strategies associated with successful collision avoidance, gaze-related parameters are depicted graphically as a function of participant group ($HVFD_A$ patients, $HVFD_I$ patients, and normal subjects) for density 50% (Fig. 4) and density 75% (Fig. 5). The mean gaze eccentricity is shown for both densities in Fig. 6. The effect of "group" under both traffic densities was significant for all examined parameters except for fixation number at both densities, and mean fixation duration at density 50% (numeric values are reported in Appendix 2). Results of post hoc tests for both densities are presented in Appendices 3 and 4 (numeric values). In comparison to $HVFD_I$ patients, visual exploration of $HVFD_A$ patients at both traffic densities was characterized by longer scanpaths, more gaze shifts, larger mean gaze eccentricity, more fixations on virtual vehicles, less "straight-ahead" fixations on the intersection (Figs. 4–6) and larger saccadic amplitudes towards both hemifields (Fig. 7). There were no significant differences between $HVFD_A$ and $HVFD_I$ patients regarding total fixation number, fixation duration (Figs. 4 and 5), proportion of fixations and proportion of gaze eccentricity to the blind hemifield (Fig. 7). Overall, visual exploration behavior was intensified in the subgroup of adequately performing patients ($HVFD_A$).

Normal subjects and $HVFD_A$ patients shared many similarities regarding their gaze patterns and differed only in a few parameters. In comparison to normal subjects, $HVFD_A$ patients exhibited larger mean gaze eccentricity and more fixations on vehicles, presumably resulting in identification of the collision-relevant ones and successful collision avoidance. Additionally, a higher proportion of fixations and gaze eccentricity, and shorter saccades to the blind hemifield were evident for $HVFD_A$ patients. Interestingly, when mean gaze eccentricity is plotted over distance to the intersection, $HVFD_A$ patients display increased values (i.e. more scanning activity) especially in the first and middle part of the route (Fig. 6b and d), which indicates the importance of gaining an initial overview of the scene.

On the other hand, normal subjects and $HVFD_I$ patients exhibited distinct gaze patterns. All examined gaze-related parameters (except for fixation number and mean fixation duration) were significantly different between these two subgroups.

3.4. Comparison of gaze-related parameters between traffic density 50% and 75%

The effect of task difficulty on scanning strategies was investigated by comparing gaze-related parameters between the two traffic densities (Table 1). Under more challenging task conditions (i.e. traffic density 75%) all three participant subgroups increased the total number of fixations and fixations on vehicles as expected. $HVFD_A$ patients and normal subjects increased their scanpath length, number of gaze shifts and mean gaze eccentricity. Fixation duration and fixations on the intersection were decreased. Interestingly, normal subjects' saccades to their left hemifield were larger for density 75% than for density 50% (Table 1). At traffic density 75% $HVFD_I$ patients displayed similar adaptive visual behavior.

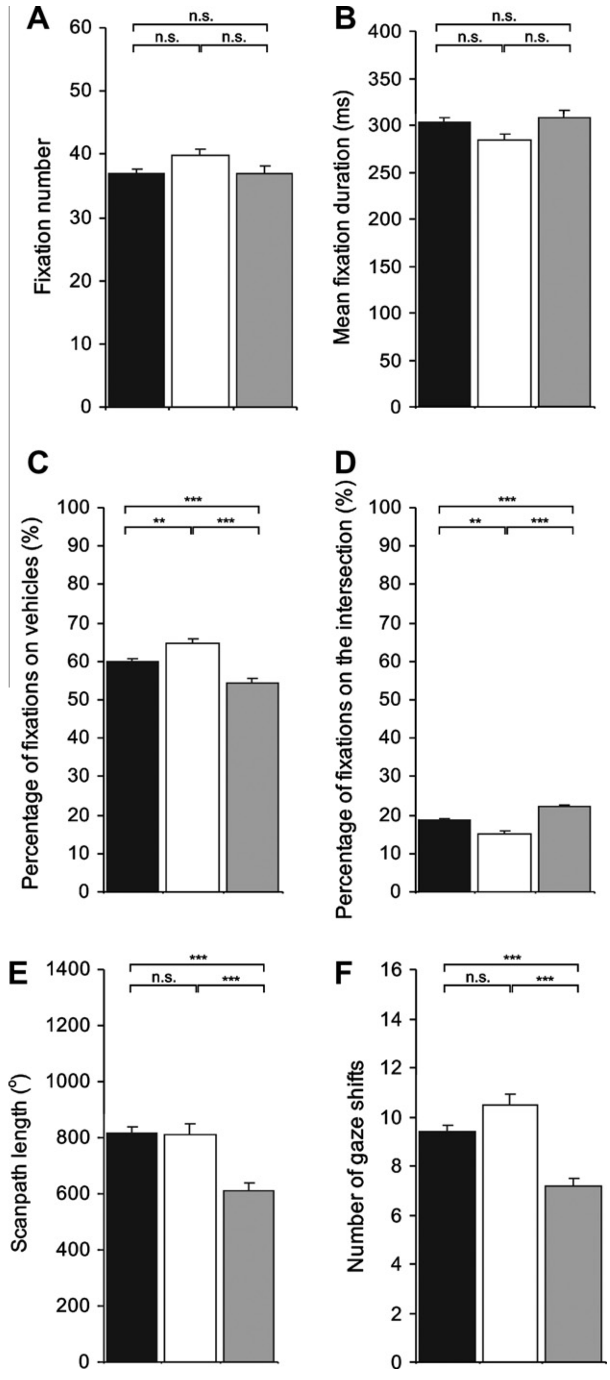

Fig. 4. Gaze-related parameters for traffic density 50%. Comparisons were performed between normal subjects (black bars), adequate-$HVFD_A$ patients (white bars) and inadequate-$HVFD_I$ patients (grey bars) regarding the number of fixations (A), mean fixation duration (B), the percentage of fixations to vehicles (C), the percentage of fixations to the intersection (D), the scanpath length (E), and the number of gaze shifts (F). Tukey's post hoc test was conducted in order to detect significant differences between groups ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons). Error bars indicate standard error of the mean (sem).

Additionally, the amplitudes of saccades directed to the blind hemifield were increased; at the same time, however, the proportion of fixations and gaze eccentricity to the blind hemifield were significantly decreased (Table 1). An overview of gaze trajectory and visual adaptations during an entire trial for a normal subject, a $HVFD_A$ patient and a $HVFD_I$ patient is given in Fig. 8 for both traffic densities.

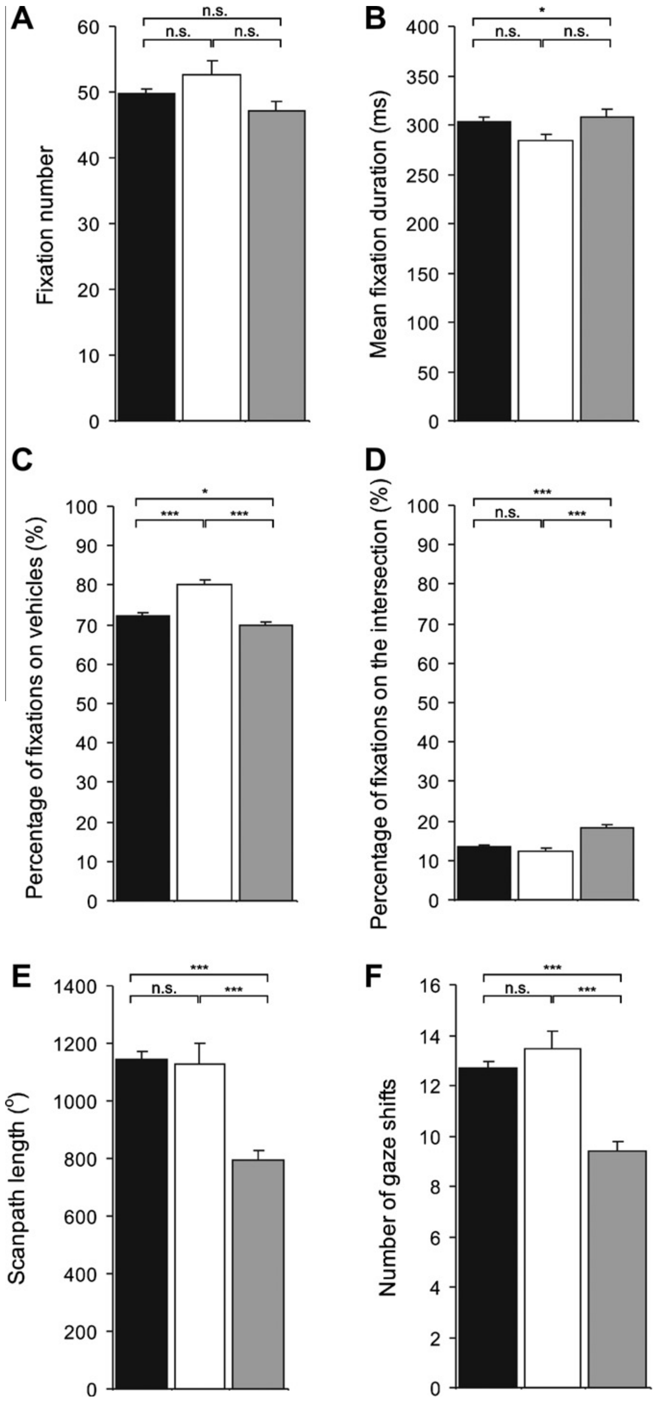

Fig. 5. Gaze-related parameters for traffic density 75%. Comparisons were performed between normal subjects (black bars), adequate-HVFD$_A$ patients (white bars) and inadequate-HVFD$_I$ patients (grey bars) regarding the number of fixations (A), mean fixation duration (B), the percentage of fixations to vehicles (C), the percentage of fixations to the intersection (D), the scanpath length (E), and the number of gaze shifts (F). Tukey's post hoc test was conducted in order to detect significant differences between groups ($^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons). Error bars indicate standard error of the mean (sem).

3.5. Hemispace analyses (comparison of gaze-related parameters between the two hemifields)

Finally, the data were analyzed to assess whether the blind hemifield was explored more than the seeing hemifield (Table 2). Both HVFD$_A$ and HVFD$_I$ patients showed similar (increased) numbers of fixations and a higher proportion of gaze eccentricity to the blind hemifield compared to their intact hemifield at both traffic densities. However, they differed in their fixation distribution. HVFD$_A$ patients devoted more fixations on vehicles and fewer fixations on the intersection than HVFD$_I$ patients. Directional analysis revealed that the mean saccadic amplitude towards the blind hemifield was significantly shorter in comparison to the seeing hemifield for both patient subgroups, while there were no differences for normal subjects (Table 2). Interestingly, normal subjects displayed more fixations in the right than the left hemifield for density 50%, and a higher proportion of gaze eccentricity to the left than the right hemifield for density 75%.

3.6. Summary of results

The main results are summarized in Fig. 8, where the gaze trajectories of a normal subject (A and D), a HVFD$_A$ patient with right homonymous hemianopia (B and E), and a HVFD$_I$ patient with right homonymous hemianopia (C and F) are shown during an entire trial at traffic density 50% (top panel) and 75% (bottom panel). Striking differences are evident between the HVFD$_A$ patient, who displays an active gaze pattern with appropriate behavioral adaptation (speed adjustments), and the HVFD$_I$ patient, who is unable to compensate. The HVFD$_A$ patient (B and E) shows more gaze shifts, more fixations on vehicles, larger saccades, larger mean gaze eccentricity – especially in the initial part of the route – and more speed adjustments (kinks) than the HVFD$_I$ patient (C and F), who demonstrates decreased gaze activity (C and F) resulting in a collision (F). Trial duration is similar between the normal subject and the HVFD$_A$ patient, while the HVFD$_I$ patient completes trials in a shorter period of time but ends in a collision (F) due to the lack of gaze movements and appropriate speed adjustments.

Table 3 provides an overview of the main compensation mechanisms (gaze-related parameters), which are implemented by hemianopic patients under three experimental tasks of increasing difficulty. The same patient population performed a dot-counting task, a comparative visual search task and the present dynamic collision avoidance task (Hardiess et al., 2010; Papageorgiou et al., 2012). In order to compensate for the visual field defect, patients use different gaze strategies, which are gradually intensified as task complexity increases.

4. Discussion

We investigated the scanning strategies of patients with HVFDs and normal subjects under dynamic VR conditions. We found that the subgroup of patients who adapt successfully to their visual deficit (HVFD$_A$), display distinct gaze patterns characterized by increased exploration, particularly towards moving objects of interest on their blind side. This compensatory behavior becomes especially evident during the more demanding task, i.e. the high traffic density condition. A gaze bias to the blind hemifield – in terms of proportion of fixations and gaze eccentricity – is observed in both patient subgroups; however, adequately compensating patients undertake longer saccades and more gaze shifts than inadequate patients, bring more visual elements into their seeing hemifield and hence display a mean gaze eccentricity that is even larger than that of normal subjects (Figs. 6 and 8).

4.1. Compensatory gaze strategies

Our findings are to some extent consistent with previous studies. It has been demonstrated that compensatory efforts of patients with HVFDs in stationary scenarios include increased numbers of fixations, longer search times and more time looking towards their

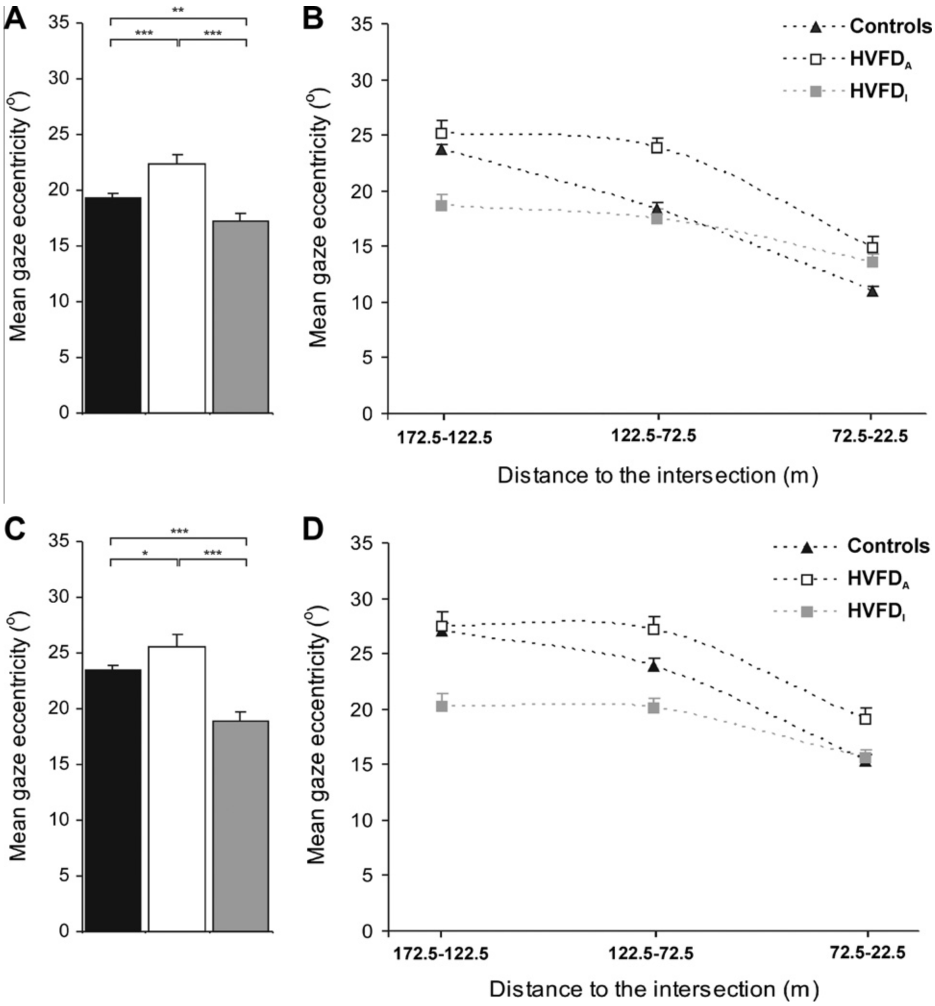

Fig. 6. Overall mean gaze eccentricity (A and C) and mean gaze eccentricity plotted over distance to the intersection for traffic density 50% (B) and 75% (D). Here, values are depicted for the first (172.5–122.5 m), the second (122.5–72.5 m) and the third (72.5–22.5 m) part of the route. Comparisons were performed between normal subjects (black bars), adequate-$HVFD_A$ patients (white bars) and inadequate-$HVFD_I$ patients (grey bars). Tukey's post hoc test was conducted in order to detect significant differences between groups ($^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons). Error bars indicate standard error of the mean (sem).

blind hemifield (Hardiess et al., 2010; Ishiai, Furukawa, & Tsukagoshi, 1987; Pambakian et al., 2000; Tant et al., 2002b). According to our results, under dynamic, time-constrained situations, the deviation of fixation distribution towards the blind side is sufficient only when it results from appropriate "goal-relevant" gaze movements, in order to extract all the necessary information for completion of the current task in a timely manner. Increased gaze scanning led to a more efficient fixation pattern for $HVFD_A$ patients, who exhibited more fixations on vehicles and fewer fixations on the intersection than $HVFD_I$ patients. This strategy resulted in identification of the collision-relevant vehicles and successful collision avoidance. Experiments on visual behavior of hemianopes in naturalistic tasks have indeed revealed that in dynamic or complex environments, where patients cannot exclusively rely on their spatial working memory in order to locate salient objects (Hardiess et al., 2010; Martin et al., 2007), compensation is possible by means of exploratory gaze movements (Fig. 9). This is reflected in the increased scanpath length, number of gaze shifts and especially in the number of fixations on vehicles and mean gaze eccentricity, where the values of the two latter parameters for $HVFD_A$ patients exceed even those of normal subjects. Similar results were obtained from on-road tests (Kooijman et al., 2004; Wood et al., 2011), showing that patients rated as safe to drive compensated by making more head movements into their blind field and received superior ratings regarding eye movements. Additionally, we observed that the mean gaze eccentricity of $HVFD_A$ patients was larger in the first and middle part of the route compared to that of normal subjects (Fig. 6). Starting to scan the visual scene at a larger distance to the intersection has been also reported in an earlier study and offers the advantage of capturing more visual elements by performing shorter saccades and also having more time to plan the motor response (Kooijman et al., 2004).

The need to compensate by gaze scanning in the context of a dynamic scenario and visual field loss is further reflected in the finding that $HVFD_A$ patients exhibit similar or even fewer fixations on the intersection than normal subjects. Normal subjects are able to parafoveally perceive and spatially represent large areas. Therefore, when they look straight ahead, input from the peripheral visual field possibly combined with spatial memory information, enables them to use the concluding milliseconds of a fixation (Pambakian et al., 2000) to program their next saccade (Hayhoe & Ballard, 2005). Preplanning of future saccades based on peripheral information has the advantage of guiding saccades to task-relevant objects, clustering neighboring stimuli and omitting empty or irrelevant parts (Tant et al., 2002b; Zihl, 1999). However, HVFD patients lack unilateral peripheral visual input that could guide their saccades, so they must explore even irrelevant parts of the visual scene, in order to increase their possibilities of detecting an

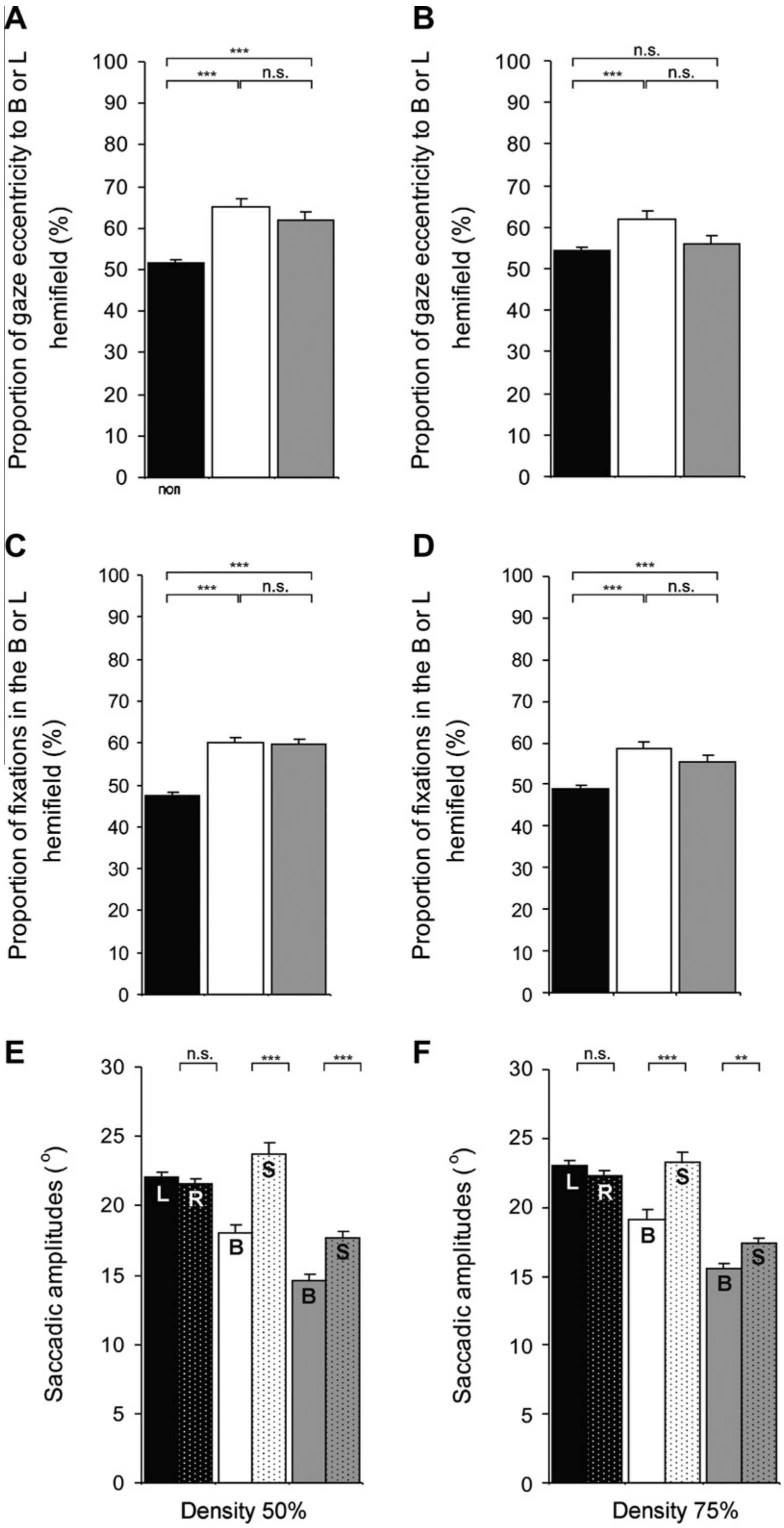

Fig. 7. Hemispace analyses for traffic density 50% (A, C and E) and 75% (B, D and F). Comparisons were performed between normal subjects (black bars), adequate-$HVFD_A$ patients (white bars) and inadequate-$HVFD_I$ patients (grey bars) regarding the proportion of gaze eccentricity to the blind-B or left-L hemifield (A and B), the proportion of fixations in the blind-B or left-L hemifield (C and D) and the gaze amplitudes to the blind-B or left-L hemifield (E and F). Tukey's post hoc test was conducted in order to detect significant differences between groups ($^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons). Unpaired *t*-tests were performed for comparisons between blind-B and seeing-S hemifield for patients, and between left-L and right-R hemifield for normal subjects. Error bars indicate standard error of the mean (sem).

object of interest, i.e. a collision-relevant vehicle in the present task (Chédru, Leblanc, & Lhermitte, 1973; Tant et al., 2002b). $HVFD_A$ patients achieve this goal by performing numerous gaze movements and shifting their gaze towards the blind hemifield.

Interestingly, although distinct differences were observed in fixation position, fixation duration was similar across the three participant groups (except for the longer fixation duration of $HVFD_I$ patients in comparison to normal subjects for the more demanding

Table 1
Gaze-related parameters, directional and hemispace analyses for normal subjects (N), $HVFD_A$ and $HVFD_I$ patients for both density conditions (mean). Statistical comparisons were made between density 50% – density 75% (matched pairs *t*-test). Bonferroni: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons.

Parameter	N			$HVFD_A$			$HVFD_I$		
	Density 50%	Density 75%	*p*	Density 50%	Density 75%	*p*	Density 50%	Density 75%	*p*
Mean number of collisions[a]	1.53	7.33	***	1.07	7.47	***	4.13	10.67	***
Total number of fixations[a]	36.99	49.66	***	39.76	52.66	***	36.99	47.15	***
Mean fixation duration (ms)[a]	302.87	261.34	***	283.91	267.39	**	307.71	285.46	**
Percentage of fixations on vehicles (%)	59.82	72.4	***	64.59	80.22	***	54.54	69.65	***
Percentage of fixations on the intersection (%)	18.52	13.42	***	15.16	12.16	***	22.08	18.45	***
Scanpath length (°)	816.31	1146.08	***	810.83	1126.21	***	610.76	793.38	***
Number of gaze shifts	9.42	12.71	***	10.5	13.45	***	7.16	9.4	***
Mean gaze eccentricity (°)	19.26	23.48	***	22.38	25.59	***	17.22	18.88	***
Trial duration (s)	15.82	22.10	***	15.03	20.61	***	14.24	18.64	***
Directional analysis									
Saccadic amplitude (°) to the blind or left hemifield	22.03	22.99	**	18.06	19.05	n.s.	14.58	15.59	**
Saccadic amplitude (°) to the seeing or right hemifield	21.58	22.28	n.s.	23.77	23.23	n.s.	17.69	17.35	n.s.
Hemispace analysis									
Proportion of fixations in the blind or left hemifield (%)	47.47	49.19	n.s.	59.88	58.71	n.s.	59.52	55.45	**
Proportion of gaze eccentricity to the blind or left hemifield (%)	51.46	54.41	*	65.02	62.00	n.s.	61.94	55.89	**

[a] Mann–Whitney U test (paired samples).

task) (Fig. 5). Our results are in general accord with studies reporting that the mean fixation duration during visual search is 275 ms (Rayner, 1998). Some authors have reported increased fixation duration for patients with HVFDs in comparison to normal subjects under stationary conditions (Hardiess et al., 2010; Machner et al., 2009; Zihl, 1999). This finding might be attributed to the lack of time constraints and the opportunity for greater reliance on working memory. In contrast to stationary displays, the processing of motion by the faster magnocellular channel (Livingstone & Hubel, 1988) in combination with time constraints in our paradigm, where participants did not have the possibility to stop the vehicle, may explain the adoption of fixations with similar duration to those of normal subjects. This result is in accordance with a study reporting eye movements of drivers while they watched films of dangerous driving situations. Similarly, the most visually complex urban roads attracted the shortest fixation durations (Chapman & Underwood, 1998).

In general, it seems plausible that poor performance of $HVFD_I$ patients should be mainly attributed to deficient implementation of gaze saccades, as also shown in a previous visual search task. Saccadic metrics accounted for much more of the variability and improvement in performance than did fixation duration. Therefore, the authors hypothesized that the speed of visual scanning depends upon how much is perceived during a single fixation, rather than how long it takes to process what is seen during that fixation (Phillips & Edelman, 2008).

4.2. Increased working memory involvement

In some recent studies no gaze bias towards the blind hemifield or adaptive gaze behavior of HVFD patients were observed, when assembling wooden models under naturalistic conditions (Martin et al., 2007) or during a dot-counting task and a comparative visual search task (Hardiess et al., 2010). It was therefore hypothesized that the static nature or the relative simplicity of these tasks afforded an opportunity for greater reliance on visuo-spatial memory (Hardiess et al., 2010; Martin et al., 2007). However, in contrast to these stationary displays, the dynamic nature of the present task forces $HVFD_A$ patients to adopt appropriate gaze strategies (Fig. 9). Recent evidence (Schuett et al., 2009) further suggests that efficient oculomotor adaptation to visual field loss is highly specific and task-dependent; therefore the dissociation in compensational strategies between various tasks should be interpreted in the light of their cognitive demand. Tasks on stationary displays, such as dot-counting (Zihl, 1999), visual search for targets and comparative visual search (Hardiess et al., 2010) require lower levels of cognitive demand than collision avoidance. Collision avoidance is a cognitively complex task, involving processes such as oculomotor adaptation, speed estimation, selection of collision relevant obstacles, storage in visual working memory and visuo-motor calibration (Lee, 1976; Simpson, Johnston, & Richardson, 2003). Therefore a distinct, highly effective compensatory strategy is expected (Fig. 9).

Our findings may suggest that gaze adaptation is the primary compensatory mechanism to achieve collision avoidance, but implementation of intact working memory should be also considered. A task-dependent representation of dynamic objects within working memory was found in normal subjects using the same collision avoidance task (Hardiess & Mallot, 2010). A limited number of collision relevant vehicles were represented preferentially in visuospatial working memory, while the distribution of gaze did not reflect the collision-relevance of vehicles (Hardiess & Mallot, 2010). Due to the visual field deficit, HFVD patients need to invest additional effort in visual search of the scene in order to select the task-relevant (i.e. collision-prone) vehicles, which will be represented in working memory (Fig. 9). Problematic visual scanning or reduced working memory capacity lead to inadequate compensation (Fig. 9). A further compensatory option for $HVFD_A$ patients is to use their intact working memory in order to perform memory-guided saccades, particularly towards the blind hemifield, where no visual input is available. By shifting their gaze to remembered coordinates of the visual scenery in a goal-oriented manner, they are able to spare time and avoid unnecessary visual search.

Storage in unimpaired working memory may also play a role for stationary elements of the visual scene, i.e. the location of the intersection (Hardiess et al., 2010; Machner et al., 2009; Martin et al., 2007). $HVFD_A$ patients efficiently avoided collisions at the intersection, although – especially for the easier task – they performed fewer fixations on it than $HVFD_I$ patients and normal subjects. $HVFD_I$ patients attempted to compensate by increased working memory involvement, as indicated by the slightly longer fixations compared to normal subjects for density 75% (Fig. 5). However, reduced working memory capacity probably forced them to devote a high proportion of their fixations on the intersection in

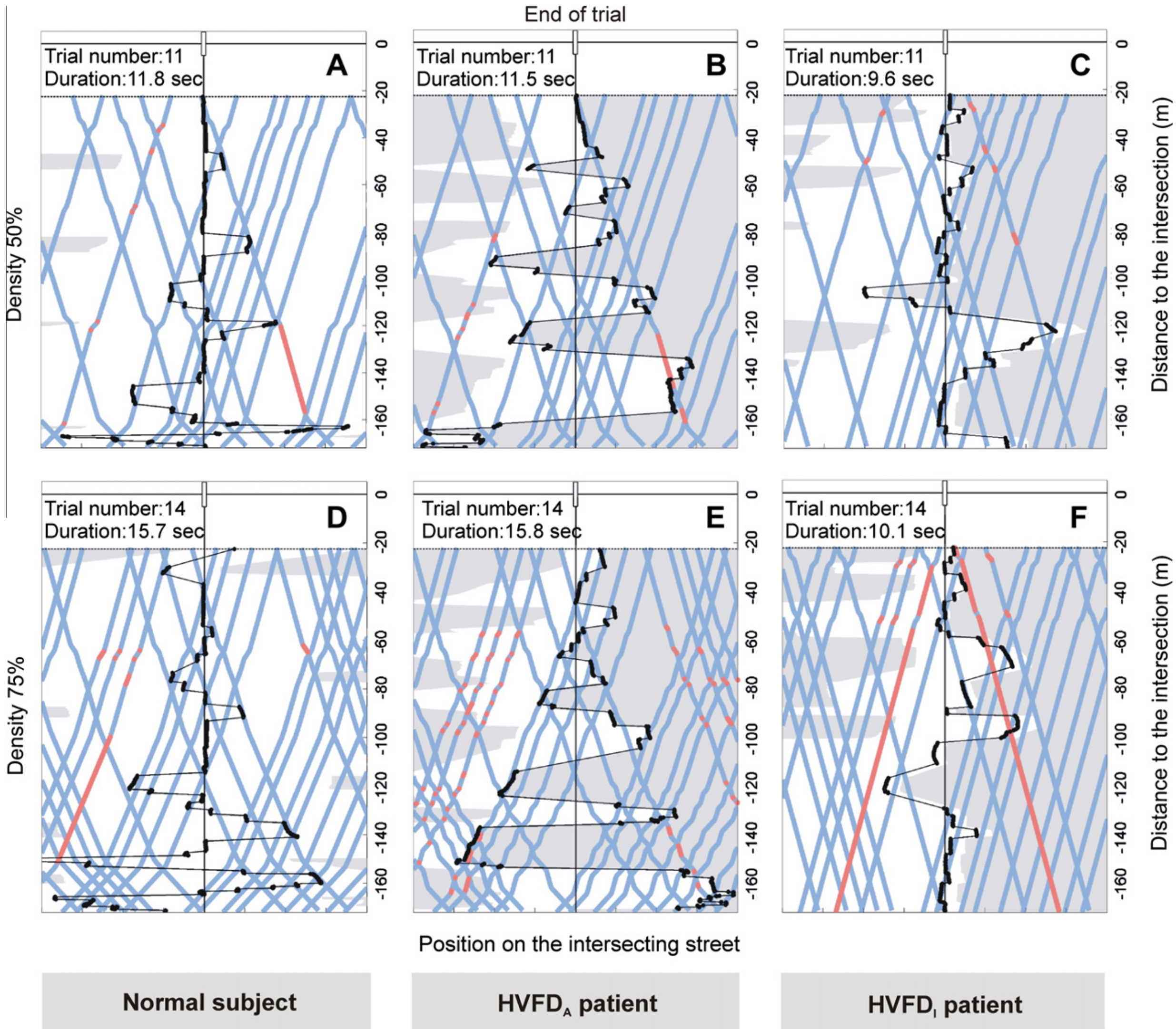

Fig. 8. Visualization of gaze trajectory. Each figure part demonstrates the participant's gaze pattern for an entire trial, from position −172.5 m (bottom = start) to position −22.5 m (top = end of intersection) in the vertical axis for traffic density 50% (top panel; trial number 11) and density 75% (bottom panel; trial number 14). Trial duration (in s) is reported on the left upper corner of each figure part. Gaze position is depicted as a black line. A normal subject (A and D), an adequate-$HVFD_A$ patient with right homonymous hemianopia (B and E), and an inadequate-$HVFD_I$ patient with right homonymous hemianopia (C and F) are shown. The grey transparent area corresponds to the visual field defect ("blind" area) and denotes the outer visual field boundaries. The blue lines represent the courses of the cross traffic vehicles and the red segments indicate vehicles moving on collision route. Speed adjustments of the participant (acceleration or deceleration) result in changes of the test vehicle position in relation to the cross traffic vehicles, and are shown as kinks on the blue lines. The $HVFD_A$ patient (B and E) shows more gaze shifts, more fixations on vehicles, larger saccades, larger mean gaze eccentricity – especially in the initial part of the route – and more speed adjustments (kinks) than the $HVFD_I$ patient (C and F), who demonstrates decreased gaze activity (C and F) resulting in a collision (F). Trial duration is similar between the normal subject and the $HVFD_A$ patient, while the $HVFD_I$ patient completes trials in a shorter period of time.

Table 2

Directional and hemispace analyses for normal subjects (N), $HVFD_A$, and $HVFD_I$ patients in both hemifields (mean). Statistical comparisons were made between blind (B) and seeing (S) hemifield for patients, and between left (L) and right (R) hemifield for normal subjects (unpaired *t*-test). Bonferroni: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, n.s. indicates non-significant comparisons.

Parameter	N				$HVFD_A$				$HVFD_I$			
	Density 50%	*p*	Density 75%	*p*	Density 50%	*p*	Density 75%	*p*	Density 50%	*p*	Density 75%	*p*
Saccadic amplitude (°) to the B or S (L or R)	22.03/ 21.58	n.s.	22.99/ 22.28	n.s.	18.06/ 23.77	***	19.05/ 23.23	***	14.58/ 17.69	***	15.59/ 17.35	**
Proportion of fixations (%) in the B or S (L or R)	47.47/ 52.53	***	49.19/ 50.81	n.s.	59.88/ 40.12	***	58.71/ 41.29	***	59.52/ 40.48	***	55.45/ 44.55	***
Proportion of gaze eccentricity (%) to the B or S (L or R) hemifield	51.46/ 48.54	*	54.41/ 45.59	***	65.02/ 34.98	***	62.00/ 38.01	***	61.94/ 38.06	***	55.89/ 44.11	***

Table 3
Gaze-related parameters for $HVFD_A$ and $HVFD_I$ patients under three experimental tasks of increasing difficulty. The italicized cells indicate significant differences between patients and normal subjects. Compensatory gaze strategies of hemianopic patients are gradually intensified as task complexity and cognitive demand increase. Data are presented as mean (standard error of the mean).

Parameter	Dot counting task				Comparative visual search				Collision avoidance (50% density)				Collision avoidance (75% density)			
	$HVFD_A$		$HVFD_I$		$HVFD_A$		$HVFD_I$		$HVFD_A$		$HVFD_I$		$HVFD_A$		$HVFD_I$	
Total number of fixations	26.8	(2.3)	33.5	(1.7)	44.6	(1.4)	51.2	(2.0)	39.76	(1.17)	36.99	(1.07)	52.66	(2.05)	47.15	(1.39)
Fixation duration (ms)	279.3	(11.1)	293.9	(9.9)	235.5	(2.5)	258.2	(2.6)	283.91	(6.06)	307.71	(8.35)	267.39	(4.89)	285.46	(8.88)
Scanpath length (°)	237.4	(22.0)	335.0	(22.8)	1180.0	(30.3)	1077.2	(43.1)	810.83	(38.45)	610.76	(28.17)	1126.21	(71.15)	793.38	(33.82)
Number of gaze shifts	–	–	–	–	16.9	(0.4)	14.8	(0.8)	10.5	(0.44)	7.16	(0.31)	13.45	(0.7)	9.4	(0.41)
Proportion of fixations in the blind or left hemifield (%)	57.5	(2.5)	63.0	(3.0)	54.9	(0.7)	58.9	(0.9)	59.88	(1.53)	59.52	(1.24)	58.71	(1.36)	55.45	(1.41)
Saccadic amplitude (°) to the blind or left hemifield	8.3	(0.3)	8.0	(0.5)	27.8	(0.4)	23.4	(1.1)	18.06	(0.51)	14.58	(0.42)	19.05	(0.74)	15.59	(0.38)

order to create an adequate spatial representation of stationary elements at the cost of moving ones (Fig. 9).

4.3. Effect of task difficulty on visual adaptation

In the more complex task (traffic density 75%) we observed increased gaze adaptation due to the higher visual demands. The participants must acquire a greater amount of relevant information in the same period of time, therefore all parameters associated to gaze movements, i.e. fixation number, fixations on vehicles, gaze shifts and scanpath length, display increased values. These findings in combination with shorter fixation duration support a greater reliance of $HVFD_A$ patients and normal subjects on gaze adaptation in order to solve the more difficult task. Fixation duration has been shown to reflect ongoing processing in scene viewing (Henderson & Graham, 2008) and shorter fixation duration has been associated with lower memory load (Velichkovsky, Challis, & Pomplun, 1995). Therefore, $HVFD_A$ patients and normal subjects seem to reduce their working memory load, as indicated by the fewer fixations on the intersection and their shorter duration, and increase their gaze adaptation in the more complex task. A possible explanation is that the plethora of moving objects does not allow the maintenance of a reliable spatial representation. Although $HVFD_I$ patients also reduce fixation duration in the more complex task, they fail to undertake enough scanning movements and to reduce their fixations on the intersection to the same degree as $HVFD_A$ patients and normal subjects. Decreased gaze activity and reduced working memory availability result in their inability to solve the task.

4.4. Saccadic metrics

In general accord with previous reports, saccadic amplitudes of patients with HVFDs in the direction of their blind field were shorter than those towards their seeing field and those of normal subjects (Ishiai, Furukawa, & Tsukagoshi, 1987; Hardiess et al., 2010; Pambakian et al., 2000; Tant et al., 2002b; Zihl, 1995, 1999). The overshooting/corrective saccade strategy towards the blind hemifield – as described previously (Meienberg et al., 1981; Zangemeister et al., 1998) – was not observed in the present study. However, $HVFD_A$ patients performed significantly longer saccades to both hemifields than $HVFD_I$ patients. There were no differences in macular sparing between the two patient subgroups, so it is unlikely that $HVFD_A$ patients received visual input from their remaining intact visual field. Saccades into the blind hemifield are based on spatial memory and allow for normal saccadic accuracy towards static targets (Martin et al., 2007). However in case of numerous moving stimuli, we assume that creating and updating of a spatial representation interferes with gaze scanning. As discussed above, given that working memory is intact in $HVFD_A$ patients, implementation of memory-guided saccades may explain the finding that $HVFD_A$ patients perform hypometric saccades towards the blind side, which however are larger – and maybe more precise – than those of $HVFD_I$ patients.

4.5. Task design

In contrast to real traffic scenarios, where drivers can and have to stop in front of an intersection, our participants were automatically driven across the intersection with the last adjusted speed, without further visual input or information about the success of the trial. Although the available period to react at an intersection is not always unlimited even in real world, our study was designed in order to achieve repeatable and completely programmable experimental conditions. Additionally, the motivation of participants should remain identical throughout the whole experiment and should not be influenced by negative feedback after a collision, especially at the difficulty level of 75%. Furthermore, implementation of higher

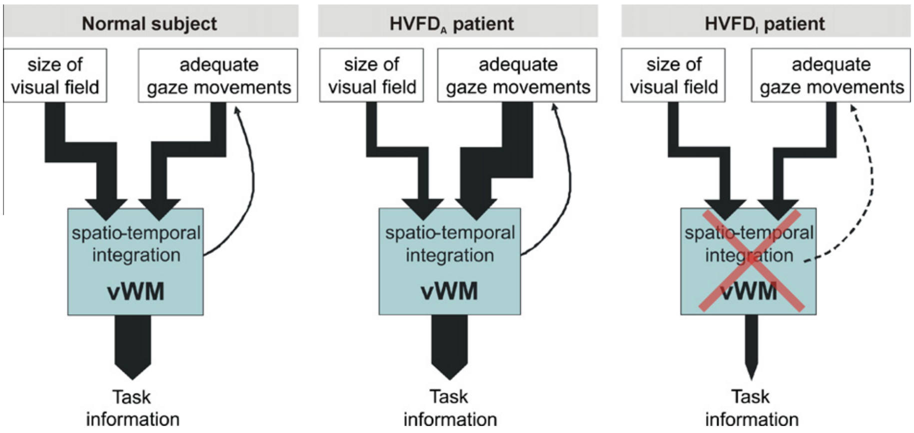

Fig. 9. A proposed model for compensatory strategies of normal subjects, $HVFD_A$ patients and $HVFD_I$ patients under dynamic, virtual reality environments. Patients lack unilateral peripheral visual field input. Increased exploration by means of eye and head movements allows adequate uptake of visual information by $HVFD_A$ patients. Subsequent integration of information in intact visual working memory (vWM) enables successful compensation. On the other hand, reduced working memory availability and lack of gaze movements in $HVFD_I$ patients are associated with ineffective visual adaptation.

cognitive processes, such as learning effects, should be possibly avoided, because aim of this study was to investigate visual performance and gaze movements. For these reasons, the number of collisions in this study may be overestimated and is not representative of real-life, but offers a performance measure, which allows for comparison between participants. By using this specific design, we aimed to assess only those gaze parameters which are relevant for the passage of an intersection.

4.6. Multimodal approach

The introduction of this dynamic collision avoidance task completed our former study on hemianopic gaze adaptations under static scenarios (Hardiess et al., 2010). This multimodal approach demonstrates the need for a gradual increase in compensatory efforts with increasing task demands (Table 3). Dot-counting restricts visual scanning to the processes of visual sampling without any further identification component (Zihl, 1999) and a low demand for working memory. The visual search for targets among distractors requires additional object recognition. Comparative visual search further involves a comparator mechanism (Hardiess et al., 2010). Collision avoidance is even more challenging, since detection of dynamic objects and appropriate response are needed (Papageorgiou et al., 2012). Our findings suggest that hemianopic compensation is different between static and dynamic displays and requires additional or more intense gaze strategies with increasing task complexity.

5. Conclusion

In conclusion, the assignment of patients into two subgroups on the basis of their performance in a collision avoidance task, allowed associating certain compensatory mechanisms with functional outcomes. Striking differences were revealed between adequately ($HVFD_A$) and inadequately ($HVFD_I$) compensating patients and normal subjects. Successful compensation was associated with active exploration in terms of more gaze shifts, increased scanpath length and longer saccades especially towards objects of interest in the blind side. Recent studies have shown that in stationary displays patients with HVFDs might compensate by means of increased working memory involvement. In addition to this evidence, our findings suggest that in the context of a dynamic environment gaze adaptation should be also implemented, in order to allow continuous updating of moving objects' spatial location and selection of the task-relevant ones (Fig. 9).

By assessing eye and head movements, this study enables better understanding of hemianopic driving behavior and confirms the qualitative observations of previous on-road studies, which showed that some hemianopic drivers compensate by exploring their blind hemifield and are therefore fit to drive compared with age-matched control drivers (Tant, Brouwer, Cornelissen, & Kooijman, 2002a; Wood et al., 2009, 2011). Virtual reality and driving simulators offer the advantage of accurate gaze tracking, but require real world validation, and their use is still not established due to lack of realism, imperfect specificity for real-life scenarios and limited availability to the general ophthalmologist. On the other hand, on-road studies are associated with safety concerns and technical difficulties regarding gaze tracking. It is obvious that neither research paradigm alone may be sufficient to study all aspects of the problem; therefore multimodal approaches that combine findings of simulator vs. on-road experiments are needed. Such studies will enhance the design of more realistic, standardized driving assessments for future use in driving simulators without any safety concerns.

Additionally, by offering insight into hemianopic gaze behavior, our findings may further enhance the development of rehabilitation tools for patients with visual field defects through training of their exploration ability (eye movements) for clinical use in hospitals and rehabilitation units. Furthermore, such an approach would be extremely useful as an interface for a specific recruitment of active safety components only if necessary, thereby avoiding any kind of "patronage". On the other hand, inefficient exploration and subsequently unsuccessful compensatory ability (for example inadequate eye movements) should lead to activation of such active safety systems.

Disclosure

Ulrich Schiefer is consultant of HAAG-STREIT, Inc., Koeniz, Switzerland, he holds patents, related to the semi-automated kinetic perimetry.

Acknowledgments

This work was supported by the following grants: European Union (PERACT-Marie Curie Early Stage Research Training, MEST-CT-

2004-504321), Deutsche Forschungsgemeinschaft (SFB 550-A4) and GRK 778.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2012.06.004.

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The neural correlates of impaired collision avoidance in hemianopic patients

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ABSTRACT.

Purpose: **The aim of this study was to assess the brain regions associated with impaired performance in a virtual, dynamic collision avoidance task, in a group of patients with homonymous visual field defects (HVFDs) because of unilateral vascular brain lesions.**

Methods: **Overall task performance was quantitatively assessed as the number of collisions while crossing an intersection at two levels of traffic density. Twenty-six patients were divided into two subgroups using the median split method: patients with 'performance *above* average' ($HVFD_A$, i.e. lower number of collisions) and patients with 'performance below average' ($HVFD_B$, i.e. higher number of collisions). In order to identify the anatomical structures that might be specifically affected in $HVFD_B$ patients but spared in $HVFD_A$ patients, overlap, subtraction and voxel-based lesion-symptom mapping analyses were performed using the MRIcron software.**

Results: **No significant difference in collision avoidance between patients with left- and right-hemispheric lesions was revealed. Separate lesion analysis in 12 patients with right- and 14 patients with left-hemispheric lesions showed that the cortical structures associated with impaired collision avoidance were the parieto-occipital region and posterior cingulate gyrus in the *right* hemisphere and the inferior occipital cortex and parts of the fusiform (occipito-temporal) gyrus in the *left* hemisphere.**

Conclusion: **In the present collision avoidance paradigm, impaired performance of patients with *right*-hemispheric lesions is associated with damage in the dorsal processing stream and potential impact on the visual spatial working memory (WM), while impaired performance of patients with *left*-hemispheric lesions is associated with damage in the ventral stream and potential impact on the visual object WM.**

Key words: cerebrovascular damage – driving – fusiform gyrus – homonymous visual field defects – lesion analysis – parieto-occipital area – posterior cingulate gyrus – virtual reality

Acta Ophthalmol. 2012: 90: e198–e205

doi: 10.1111/j.1755-3768.2011.02315.x

Introduction

Homonymous visual field defects (HVFDs) affect nearly 80% of patients with unilateral postchiasmal brain damage (Zihl 1994). HVFDs create a marked amount of subjective inconvenience in everyday life (Papageorgiou et al. 2007). Patients may show persistent and severe impairments of reading, visual exploration and navigation, collide with objects on their blind side and may be deemed unsafe to drive (Zihl 2003; Hardiess et al. 2010). It has been a matter of debate whether hemianopic patients are capable of compensating for their visual deficit and hence receiving safe ratings in on-road or simulated driving assessments (Szlyk et al. 1993; Schulte et al. 1999; Tant et al. 2002a; Bowers et al. 2009; Wood et al. 2009).

It has been suggested that the compensatory efficacy of patients with HVFDs may be related to the brain lesion site. Some authors have reported that patients with right brain damage display worse driving skills and ineffective visual search, because of the assumed specialization of the right posterior hemisphere for visuospatial function (Meerwaldt & Van Harskamp 1982; Mazer et al. 1998). However, findings from on-road and simulator driving experiments do not consistently confirm this assumption

(Szlyk et al. 1993; Tant et al. 2002a,b; Wood et al. 2009). The location of the brain lesion in regard to the driving skills of HVFD patients has been studied even less, and relevant evidence relies mainly on visual search tasks. In a dot-counting paradigm, Zihl (1995) suggested that occipito-parietal and posterior thalamic brain injury may be responsible for inefficient compensation. Recent lesion analyses provided additional evidence that brain damage involving the occipito-temporal (fusiform) and parahippocampal gyri may impair hemianopic scanning during visual search (Machner et al. 2009; Hardiess et al. 2010). Novel functional MRI (fMRI) studies have used commercially available PC driving games in order to assess the neural substrates of driving in healthy subjects (Walter et al. 2001; Calhoun et al. 2002; Uchiyama et al. 2003; Horikawa et al. 2005; Jeong et al. 2006; Spiers & Maguire 2007). Yet, studies of the effect of brain lesion location on the performance of patients with HVFDs in driving tasks are missing.

Therefore, the purpose of this study was to assess the brain regions associated with impaired performance in a simulated collision avoidance task in patients with HVFDs owing to unilateral cerebrovascular lesions. We hypothesized that patients with right-hemispheric lesions would demonstrate poorer performance in terms of collision avoidance, because of the assumed spatial function of the right hemisphere. Furthermore, the brain region associated with impaired performance would probably be the right occipito-parietal area.

Material and Methods

Subjects

Potential participants with HVFDs were recruited from the Department of Neuro-Ophthalmology and the Neurological Clinic at the University of Tübingen (Germany), as well as the Neurological Clinic of the Bürgerhospital in Stuttgart and the Bad Urach Rehabilitation Centre.

To be included in the study, all participants were required to be at least 18 years old, to have best-corrected monocular (near and distant) visual acuity of at least 16/20 and normal anterior visual pathways as evaluated by ophthalmological tests (fundus and slit-lamp examinations, ocular alignment and ocular motility). Patients should have a HVFD, because of a unilateral vascular brain lesion, which was documented by neuroradiological findings (magnetic resonance imaging or computerized tomography), varying from complete homonymous hemianopia to homonymous paracentral scotomas. Exclusion criteria for patients were as follows: visual hemi-neglect as determined by horizontal line bisection, copying of figures and by means of the 'Bells test' (Gauthier et al. 1989), evidence of cognitive decline, aphasia, apraxia, visual agnosia or physical impairment, cerebral tumour, multiple sclerosis, Alzheimer's disease, Parkinson's disease and previous visual training. The time span between the brain lesion and the examination date should be at least 6 months.

The research study was approved by the Institutional Review Board of the University of Tübingen (Germany) and was performed according to the Declaration of Helsinki. Following verbal and written explanation of the experimental protocol, all subjects gave their written consent, with the option of withdrawing from the study at any time.

Experimental procedure

Visual fields of patients were assessed with monocular threshold-related, slightly supraliminal automated static perimetry (sAS) within the central 30° visual field, binocular slightly sAS perimetry within the 90° visual field as well as binocular semi-automated 90° kinetic perimetry (SKP), each obtained with the OCTOPUS 101 Perimeter (Fa. Haag-Streit, Koeniz, Switzerland).

Performance in the dynamic, collision avoidance task was assessed under virtual reality conditions (Fig. 1). A cognitively challenging, collision avoidance task at an intersection was chosen, because safe passage at intersections may be particularly difficult for HVFD drivers, as a very wide field must be scanned (Bowers et al. 2009). By using virtual reality, it was possible to achieve standardized, repeatable experimental conditions, manipulate task demands and avoid any safety concerns and driving licensure issues encountered in previous on-road assessments (Rizzo et al. 2001).

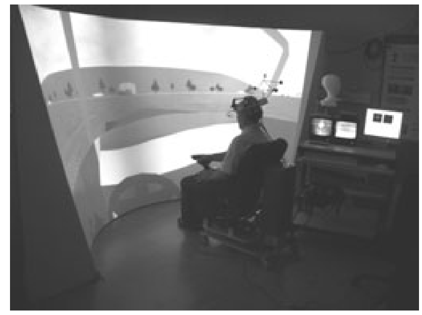

Fig. 1. Virtual reality environment. Study participant seated in front of the projection screen.

The virtual reality environment was displayed on a cone-shaped projection screen (horizontal field of view: 150° and vertical: 70°). Subjects were seated upright with the back tightly on the chair and with their head in the axis of the conical screen (eye level: 1.2 m altitude, distance to the screen: 1.62 m, Fig. 1). The virtual environment and the experimental procedures were programmed in the OpenGL Performer™ (Silicon Graphics, Inc., Fremont, CA, USA; spatial resolution: 2048×768 pixels). Subjects started each trial in a tunnel. After leaving the tunnel, they could adjust their driving speed between 18 and 61.2 km/hr (11.2–38 mph) by means of a joystick in order to avoid a collision with the cross-traffic at the intersection. During the driving period, it was not possible to stop the car. The subjects were instructed to 'drive' along a straight road (Fig. 2A,B) and finally to cross a virtual intersection without causing a collision. The driving distance to the intersection was 172.5 m, and the only possible movement of the virtual vehicle was straight ahead. When subjects reached a white line 22.5 m before the intersection (Fig. 2B), they were automatically driven across the intersection at the last adjusted speed without further visual input.

A potential collision was then calculated by the simulation programme and was delivered to the examiner at the end of the experiment. Even in case of a collision, the participants did not experience a virtual crash and did not receive any feedback about the result during the experiment, in order to maintain identical conditions for

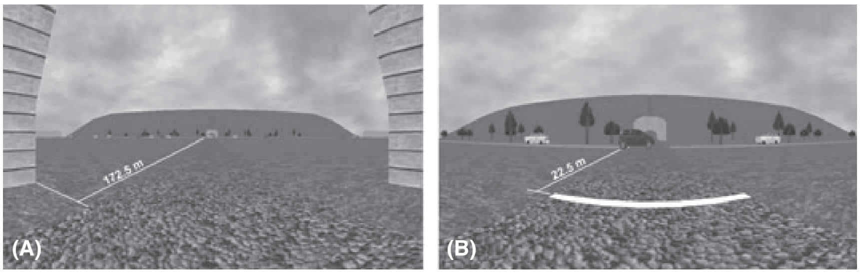

Fig. 2. Start and end positions of the virtual drive. (A) Start position of the virtual vehicle in the tunnel. The distance to the intersection is also depicted. (B) End position of the virtual drive at the white line 22.5 m before the intersection.

each trial. All cars of the cross-traffic had a constant speed of 50 km/hr (31.1 mph) and were either red Renault Twingo or white Trabant vehicles with equal numbers of cars approaching from the left side and right side. The experiment was performed at two traffic density levels of ascending difficulty, which would generate collisions in 50% or 75% of the trials respectively – assuming that a subject would begin the trial in a random time-point and would drive with random speed (i.e. with closed eyes). Subjects performed 30 trials in the same randomized order (i.e. 15 trials for each density level) and were free to perform head and eye movements. Prior to the start of the experiment, all subjects underwent a training session lasting 5–10 min. The time to complete the whole experiment ranged from 40 to 50 min.

Statistical analysis

A distinction between 'above average' (= $HVFD_A$, i.e. lower number of collisions) and 'below average' (= $HVFD_B$, i.e. higher number of collisions) patients regarding their performance in this simulated collision avoidance task was performed by the median split method (Mitchell & Jolley 2010). The square roots of the number of collisions for each density level were used to span a two-dimensional co-ordinate system, where each point represents a patient (Appendix S1). The square root transformation of the data was used in order to stabilize the variance for Poisson distributed variables. $HVFD_A$ patients were compared with $HVFD_B$ patients regarding age, gender, time since brain lesion, side of brain lesion and extent of HVFD. From the binocular semi-automated 90° kinetic perimetry (SKP), the extent of HVFD (in degrees^2) was automatically calculated for the stimulus III 4e (background luminance 10 cd/m^2 and angular velocity 3° per second) by means of a software tool available on the OCTOPUS 101 Perimeter. All data sets were tested for normality by the Shapiro–Wilk test; parametric statistics were applied for normally distributed data. For non-normally distributed data, the Mann–Whitney *U*-test was used.

Lesion mapping

For analysis of the brain lesions, patients' lesions were mapped on the individual MRI image for every single transverse slice using the MRIcron software (http://www.cabiatl.com/mricro/mricron/index.html, Rorden et al. 2007). Both the scan and lesion shape were then transferred into stereotaxic space using the spatial normalization algorithm provided by SPM5 (http://www.cabiatl.com/mricro/mricron/index.html). In order to identify the anatomical structures that were commonly affected in patients with impaired performance ($HVFD_B$) but were typically spared in patients with adequate performance ($HVFD_A$), we used the lesion subtraction analysis. This method attempts to identify the anatomical basis of a particular behaviour by comparing brain lesions of patients who exhibit the deficit of interest with patients who do not (Rorden & Karnath 2004). Lesions of patients who have the disorder ($HVFD_B$) are superimposed in an overlay plot. An overlay plot is also created for a control group of patients who do not have the disorder ($HVFD_A$), but suffer from brain lesions in the same hemisphere and are similar to the patients of interest with respect to other variables, such as other neuropsychological symptoms or visual field defects (Rorden & Karnath 2004). The two groups are then compared by performing a 'subtraction', which contrasts the experimental group of patients (lesion overlay with positive values, $HVFD_B$) with a control group (lesion overlay with negative values, $HVFD_A$). Hence, this method distinguishes regions that are often damaged in strokes from regions that are specifically required for the task of interest (collision avoidance in this case). The resulting subtraction image specifically highlights regions that are both frequently damaged in experimental patients ($HVFD_B$) and typically spared in control patients ($HVFD_A$). Lesions were plotted in an overlapping fashion onto the template brain separately for patients with left- and right-hemispheric lesions. Subtraction plots directly contrasted patients with performance 'above average' (i.e. lower number of collisions, $HVFD_A$) versus patients with performance 'below average' (i.e. higher number of collisions, $HVFD_B$).

The lesion volumes were subsequently imported into the NPM (non-parametric mapping) software, which is implemented in the MRIcron software, in order to statistically assess, on a voxel-by-voxel basis, whether a difference in the lesion location exists between $HVFD_A$ and $HVFD_B$ patients. (Rorden et al. 2007). This quantitative voxel-based lesion-symptom mapping (VLSM) analysis used the nonparametric Liebermeister test, which is performed on binomial data and thus requires patients to be assigned to two different groups ($HVFD_A$ and $HVFD_B$) based on a behavioural measure (collision avoidance performance). To control for multiple comparisons, family-wise error (FWE) rates were computed using repeated permutation tests. Only voxels damaged in at least two patients were included in the VLSM analyses. The significance threshold was set at $p < 0.05$.

Results

Thirty eligible patients with HVFDs because of unilateral brain damage were initially enrolled in the study. MRI scans were available for 26 patients, who were finally included in the analyses (age: 48.2 ± 15.9 years mean ± SD). The demographic characteristics of each of the 26 patients are listed in Appendix S2. The aetiology of the HVFD was in all cases a unilateral cerebrovascular lesion owing to ischaemia (20 patients), haemorrhage (one patient), rupture of intracerebral aneurysm (two patients), arteriovenous malformation (one patient) or haemorrhage after trauma (two patients). Time since lesion was at least 6 months, and in 81% of the patients (21 26 patients), it was at least 1 year (median: 16.6 months, range: 6 months to 16 years). There were 12 patients with right-hemispheric and 14 patients with left-hemispheric lesions.

The median split method and the division of patients into two subgroups ($HVFD_A$ 'above average' and $HVFD_B$ 'below average') were performed in the initial cohort of 30 patients for whom performance measures (number of collisions) were available (Appendix 1). This approach was followed in order to achieve a more valid patient assignment by using a larger, more representative sample of HVFD subjects. All further analyses were conducted on the 26 patients with available MRI scans, comprising 12 $HVFD_A$ and 14 $HVFD_B$ patients. $HVFD_A$ patients (age: 43.3 ± 17.4 years, mean ± SD) did not differ from $HVFD_B$ patients (age: 52.4 ± 13.6 years, mean ± SD) regarding age ($t(24) = -1.48$, p = 0.15, *t*-test) and gender (p = 0.68, Fisher's exact test for dichotomous variables). Similarly, there was no difference in the side of brain lesion (Fisher's exact test for dichotomous variables, p = 0.71) and time since brain lesion between $HVFD_A$ (median: 1.35 years, range: 6 months to 10 years) and $HVFD_B$ (median: 1.39 years, range: 6 months to 16 years) patients ($Z = -0.51$, p = 0.61, Mann–Whitney *U* test). Regarding the extent of the HVFD, $HVFD_B$ patients had larger visual field defects (median: 8109 degrees^2, range: 97 to 9881 degrees^2) than $HVFD_A$ patients (median: 3738 degrees^2, range: 114–10343 degrees^2), but this difference was of borderline significance ($Z = -1.98$, p = 0.048, Mann–Whitney *U* test). Additionally, as we have reported elsewhere (E. Papageorgiou 2011), wide variability in performance among patients with identical visual field defects suggests that visual-field-related parameters per se are inadequate in predicting successful collision avoidance. Therefore, we investigated the effect of additional parameters, such as the location of brain lesion in the present study and the role of gaze compensation in another ongoing one.

Lesion analysis was performed in order to identify the anatomical structures that might be affected in $HVFD_B$ patients but spared in $HVFD_A$ patients. Patients with right- (5 $HVFD_A$ versus 7 $HVFD_B$) and patients with left-hemispheric lesions (7 $HVFD_A$ versus 7 $HVFD_B$) were investigated separately (Figs 3 and 4). For patients with *right*-hemispheric brain lesions (Fig. 3), the centre (dark yellow and yellow) of the subtracted lesion overlap (Fig. 3C) indicated a region surrounding the parieto-occipital sulcus and involving mesial and posterior parts of the superior occipital lobe, the posterior parietal cortex and the posterior cingulate gyrus (damaged at least 40% more frequently in $HVFD_B$ patients than in $HVFD_A$ patients).

A similar analysis was performed for patients with *left*-hemispheric lesions (Fig. 4). In this case, the centre (dark yellow, yellow and white) of the subtracted lesion overlap revealed the inferior occipital cortex and the posterior part of the occipito-temporal (fusiform) gyrus that were damaged at least 40% more frequently in $HVFD_B$ patients than in $HVFD_A$ patients with left-hemispheric brain lesions (Fig. 4C).

To provide a statistical test of these results, we performed a VLSM analysis that used the assignment of patients into two subgroups ($HVFD_A$ and $HVFD_B$) as a binomial measure. The uncorrected statistical map illustrated in Fig. 5 shows brain areas that were predictors of impaired collision avoidance in HVFD patients. The analysis for right-hemispheric lesions

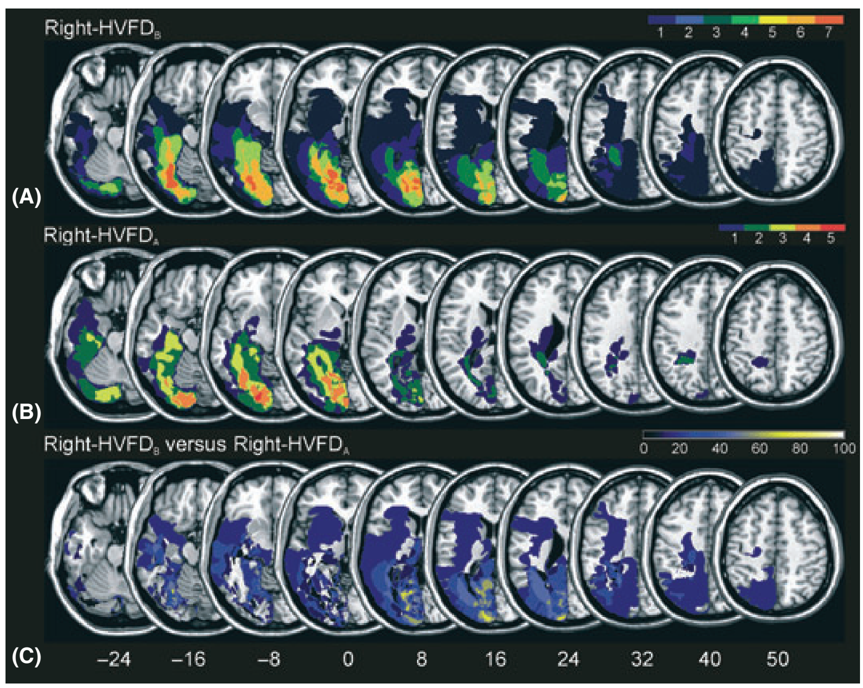

Fig. 3. Lesion analysis of patients with *right*-hemispheric lesions ('below' versus 'above' average performance). (A, B) Simple lesion overlay plots, which show the degree of involvement of each voxel in the lesions of the group of $HVFD_B$ patients and the group of $HVFD_A$ patients. Overlapping lesions are colour-coded with increasing frequency, which indicates the absolute number of patients: from dark blue ($n = 1$) to red ($n = 7$) for $HVFD_B$ patients (A, top) and accordingly from dark blue ($n = 1$) to red ($n = 5$) for $HVFD_A$ patients (B, middle). (C) Subtraction of the superimposed lesions of $HVFD_A$ patients from the overlap image of the $HVFD_B$ patients. The subtraction plot shows colour-coded relative frequency of damage in the $HVFD_B$ group after subtraction of the $HVFD_A$ group, coding increasing frequencies from dark blue to white in bins of 20%. Yellow colour indicates regions that were damaged at least 40% more frequently in the $HVFD_B$ group than in the $HVFD_A$ group. MNI (Montreal Neurological Institute) *z*-co-ordinates of the transverse sections are given. HVFD, homonymous visual field defect.

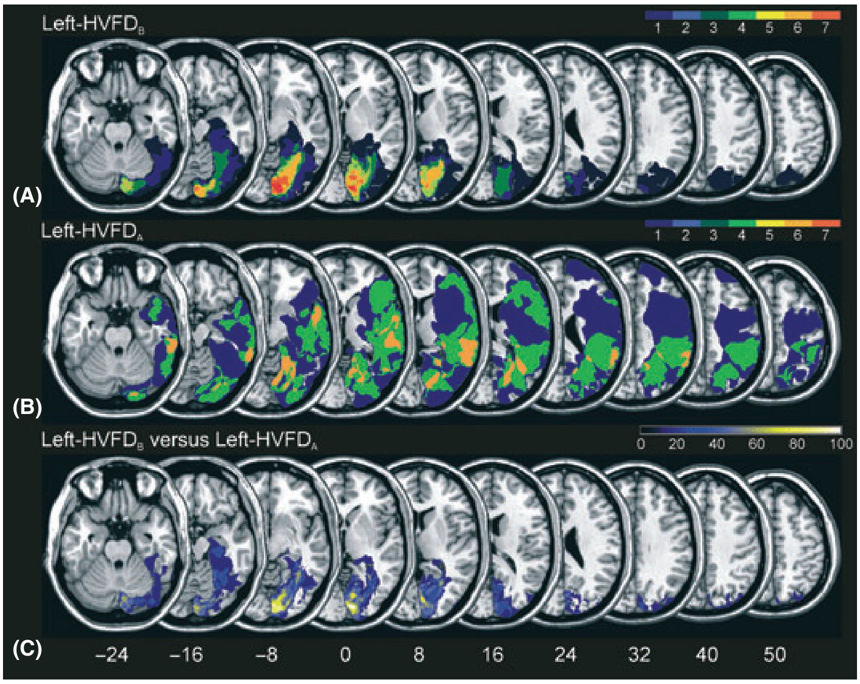

Fig. 4. Lesion analysis of patients with *left*-hemispheric brain lesion ('below' versus 'above' average performance). (A, B) Simple lesion overlay plots, for the group of $HVFD_B$ patients (A, top) and the group of $HVFD_A$ patients (B, middle). Overlapping lesions are colour-coded with increasing frequency, which indicates the absolute number of patients: from dark blue ($n = 1$) to red ($n = 7$) for both groups. (C) Subtraction of the superimposed lesions of $HVFD_A$ patients from the overlap image of the $HVFD_B$ patients. MNI *z*-co-ordinates of the transverse sections are given. HVFD, homonymous visual field defect.

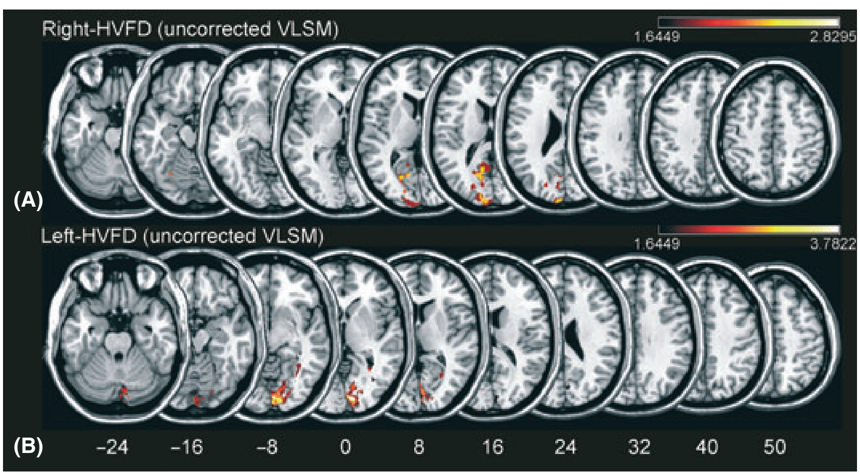

Fig. 5. Uncorrected statistical map resulting from the voxelwise analysis (the data are not adjusted for multiple comparisons). Colour bar indicates *z*-scores. Impaired collision avoidance is associated with lesions of the parieto-occipital sulcus and posterior parts of the superior occipital lobe in the right hemisphere (A, top). In the left hemisphere, the critical region involves the inferior occipital lobe (B, bottom). MNI *z*-co-ordinates of the transverse sections are given.

identified a region affecting the parieto-occipital sulcus and posterior parts of the superior occipital lobe as critical for impaired performance in the present collision avoidance task (Fig. 5A). In left-hemispheric lesions, a region in the inferior occipital lobe extending slightly anterior towards the fusiform gyrus was revealed (Fig. 5B). These regions are identical to the maximal subtracted lesion overlap (Figs 3C and 4C).

Because of the small number of patients in the present study, fewer voxels of this statistical map survived the adjustment for multiple comparisons (FWE-corrected α-level of $p < 0.05$). Nevertheless, the corrected statistical map illustrated in Fig. 6 revealed differences in the same areas as indicated by the subtraction analysis.

Discussion

In contrast to our hypothesis, no performance differences were revealed between patients with right- and left-hemispheric lesions. However, lesion analysis suggests that right-hemispheric damage in patients with performance below average ($HVFD_B$) was more frequent in the parieto-occipital region and posterior cingulate gyrus, while left-hemispheric damage in $HVFD_B$ patients was more likely to involve the inferior occipital cortex and the fusiform (occipito-temporal) gyrus. The VLSM analyses statistically confirmed the group comparisons based on lesion overlap counts and subtraction plots, although because of the small number of patients, the observed critical regions were more limited to the parieto-occipital sulcus and posterior parts of

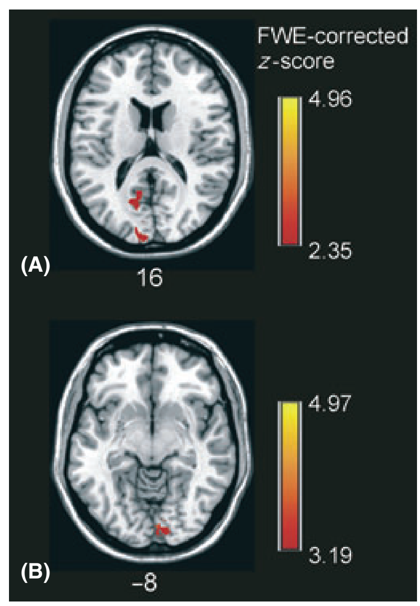

Fig. 6. Corrected statistical map showing lesion correlates of impaired collision avoidance in patients with right- (A, top) versus left-hemispheric brain damage (B, bottom). Only voxels that survived correction for multiple comparisons are shown (family-wise error-corrected α-level of $p < 0.05$). Colour bar indicates *z*-scores. MNI *z*-co-ordinates of the transverse sections are given.

the superior occipital lobe in the right hemisphere and the inferior occipital lobe in the left hemisphere.

These findings might be well explained on the basis of information processing within the visual system. A model has been proposed based on two parallel visual systems: a ventral 'perception' stream projecting from primary visual cortex to the inferior temporal lobe, which mediates object identification, and a dorsal 'action' stream, projecting from early visual areas and the superior colliculus to the posterior parietal cortex, which is dedicated to the processing of spatial information (Ungerleider & Mishkin 1982; Goodale et al. 2005). Subsequent evidence by Goodale and Milner suggested that both streams process information about the structure of objects and their spatial location, but they transform this information into quite different outputs (Milner & Goodale 1995; Goodale et al. 2005). According to their model, the ventral stream enables enduring perceptual representation of our surrounding world. By contrast, the dorsal stream is responsible for the visual control of action (Milner & Goodale 1995). There is a complex interaction between both streams, in order to produce adaptive behaviour (Goodale et al. 2005). It has been proposed that hemispheric specialization appears to have led to asymmetric elaborations of the dorsal and ventral pathways (Tucker et al. 1995). The right hemisphere processes information primarily with the more globally focused dorsal system, while the left hemisphere tends to focus on detail similarly to the ventral visual system (Tucker et al. 1995). It seems therefore plausible that worse performance of $HVFD_B$ patients with right-hemispheric lesions is associated with impairment in the dorsal stream, while worse performance of $HVFD_B$ patients with left-hemispheric lesions is probably associated with damage in the ventral stream. This interpretation could fit well in the nature of the presented driving paradigm. In a collision avoidance task with dynamic obstacles, a driver must estimate the time interval that it will take for his car to cross the road at an intersection before an oncoming vehicle will arrive there, i.e. time to collision (Lobjois et al. 2008). This task requires a visuo-motor calibration that consists of perceiving the size of the gap between the cross-traffic vehicles in terms of time to act (Lobjois et al. 2008). Recognition of collision-relevant objects in regard to their intrinsic properties (shape and colour) and relevant location, decision-making and action planning are associated with the ventral stream. Subsequently, the registration of visual information about the goal (collision avoidance) on a moment-to-moment basis, motor programming and execution in terms of adapting the speed of the vehicle or even eliciting appropriate saccadic movements towards collision-relevant objects are mediated by the dorsal stream. Ultimately then, both streams contribute to the production of goal-directed actions, in this case avoidance of collision-relevant objects, albeit in different ways and on different time scales (Goodale et al. 2005).

An additional aspect that might explain our findings is the working memory (WM) demand implicated in our paradigm. Working memory refers to the short-term maintenance, active rehearsal and manipulation of information in order to establish cross-temporal contingencies between sensory stimulation and subsequent behavioural responses (Baddeley 1986; Fuster 2001). Neuroimaging studies have revealed that the maintenance functions of visual WM are attributed to a temporo-frontal circuit assumed relevant for pattern and a parieto-frontal circuit for spatial information (Ungerleider et al. 1998; Sala et al. 2003). Similarly, in a meta-analysis on PET and fMRI studies of WM by Wager & Smith (2003), it was found that object storage tasks most frequently activated the infero-temporal cortex and spatial storage most frequently activated the parietal cortex. The same authors reported evidence for left-hemispheric lateralization of object WM and right-hemispheric lateralization of spatial WM (Wager & Smith 2003). One may speculate that as our task requires both pattern and spatial information storage, WM abilities are affected in patients with impaired performance ($HVFD_B$), targeting either the right parieto-occipital region (spatial storage) or the left occipito-temporal area (object storage).

Our results from the lesion analysis are to some extent consistent with previous studies on the performance of patients with HVFDs in visual search tasks (Machner et al. 2009; Hardiess et al. 2010). Damage in mesio-ventral areas of the temporal lobe, i.e. the occipito-temporal (fusiform) gyrus, has been associated with compromised visual search of static colour targets among distracters (Machner et al. 2009; Hardiess et al. 2010). Hence, it was suggested that deficits in colour and object recognition and reduced WM availability owing to damage in the ventral processing stream might underlie impaired performance (Machner et al. 2009; Hardiess et al. 2010). Collision avoidance in the present task requires additional WM storage of the spatial features of moving objects under continuous update of their location, and increased attentional awareness for collision-relevant objects, which might further contribute to the involvement of the right parieto-occipital area. This finding is consistent with the results of Zihl (1995) on a simple dot-counting task, who suggested that 'impaired spatial organization and integration of visual scanning in hemianopic patients was due to additional brain damage of the posterior thalamus or parieto-occipital brain areas'.

Although some authors have reported worse performance measures of patients with right-hemispheric lesions (Mazer et al. 1998), we did not find any differences in performance between patients with left- and right-hemispheric lesions in consistent with earlier studies (Ratcliff & Newcombe 1973; Szlyk et al. 1993; Zihl 1995; Tant et al. 2002a; Bowers et al. 2009; Wood et al. 2009). This is probably due to the fact that patients with clinical evidence of neglect or signs of impaired lateralized attention in the paper-and-pencil tests were excluded. As suggested recently, this may indicate that the tests used (horizontal line bisection, copying of figures and the 'Bells test') are sufficient to detect neglect symptoms (Bowers et al. 2009).

Regarding the relevance of the presented cortical structures for our collision avoidance task, several investigators by means of fMRI and PET experiments detected brain activation in the occipital and parietal regions bilaterally as neural substrates of simulated and actual driving (Walter et al. 2001; Horikawa et al. 2005; Jeong et al. 2006; Spiers & Maguire 2007). It is suggested that the above regions are concerned with visual information processing and perceptual processes associated with simulated driving (Walter et al. 2001; Jeong et al. 2006; Spiers & Maguire 2007). Interestingly, in consistent with our findings, Horikawa et al. (2005) found a significant correlation between regional cerebral blood flow in the posterior cingulate gyrus bilaterally and number of crashes during a simulated driving task. Based on earlier studies as well, they speculated that the cingulate gyrus, as a major component of the network for visuo-spatial attention (Vogt et al. 1992; Menon et al. 2001; Mesulam et al. 2001), is involved in performance monitoring during driving behaviour (Horikawa et al. 2005).

The present results must be treated with caution, because our study has some limitations: The lesion overlapping approach tends to associate a brain region with a particular function. However, evidence from cognitive neuroscience suggests, instead, that the function of a given brain region may only emerge through the interaction with other regions, in a functional network organization (Bartolomeo 2006). Particularly in the case of post-traumatic brain haemorrhage (2 of 26 patients in our sample), it has been recognized that focal and diffuse pathologies coexist. Focal changes include contusion and haematoma formation, whereas diffuse changes include diffuse axonal injury and diffuse microvascular damage. In addition, more generalized disorders involving widespread neuroexcitation and global metabolic changes are present (Povlishock & Katz 2005). This is the reason why standard MRI may underestimate the extent of brain damage, and in many cases, the location and extent of this injury does not fully explain the patient's cognitive problems (Bigler 2001). Moreover, although Jeong et al. (2006) have shown good correlations between the results of real and simulated driving, the degree of realism is limited in simulated driving. Finally, all previous fMRI experiments included healthy subjects (Walter et al. 2001; Horikawa et al. 2005; Spiers & Maguire 2007). However, recent experiments have described changes in neuronal activity of the visual cortex in patients with hemianopia, suggesting neuronal plasticity within the visual cortex after postgeniculate ischaemic lesions (Henriksson et al. 2007; Nelles et al. 2007). Therefore, analysis in a larger group of patients is needed in order to investigate Zihl (1995) suggestion that in patients with spontaneous oculomotor compensation, brain damage is limited to the optic radiation and/or the primary visual cortex, and hence to define whether strokes isolated to the occipital lobe are associated with better performance in similar driving tasks.

To summarize, we performed lesion analysis in patients with chronic HVFDs of vascular origin, who were examined in a controlled, collision avoidance driving task under virtual reality conditions. Although there are limitations regarding the number of participants and the degree of realism in the present task, lesion analysis has identified distinct brain regions responsible for impaired collision avoidance. On the other hand, the extent of the HVFD was only slightly larger in patients with poorer performance, suggesting that the visual field may be less decisive than previously thought in predicting the driving ability of patients with HVFDs in virtual reality scenarios. The first explanation supported by our findings is that brain lesion location is associated with WM availability. Additionally, brain lesion characteristics probably determine the potential for compensatory eye and head movements, which are essential features of safe driving. Therefore, patient assessment in terms of driving fitness should take into consideration not only perimetry, but also brain lesion and compensatory ability. Ideally, the link between lesion location, compensatory behaviour and effective driving remains to be determined in real on-road driving scenarios.

Acknowledgements

This study was supported by the following grants: European Union (PERACT-Marie Curie Early Stage Research Training, MEST-CT-2004-504321), Deutsche Forschungsgemeinschaft (SFB 550-A4) and Graduiertenkolleg 778. The authors are indebted to Regina Hofer and Elke Krapp (Department & Institute for Ophthalmology, Tübingen, Germany) for expert assistance with graphics.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Median split method.
Appendix S2. Patients' demographic characteristics.

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Received on February 11th, 2011.
Accepted on October 17th, 2011.

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View-Based Organization and Interplay of Spatial Working and Long-Term Memories

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Abstract

Space perception provides egocentric, oriented views of the environment from which working and long-term memories are constructed. "Allocentric" (i.e. position-independent) long-term memories may be organized as graphs of recognized places or views but the interaction of such cognitive graphs with egocentric working memories is unclear. Here we present a simple coherent model of view-based working and long-term memories, together with supporting evidence from behavioral experiments. The model predicts (*i*) that within a given place, memories for some views may be more salient than others, (*ii*) that imagery of a target square should depend on the location where the recall takes place, and (*iii*) that recall favors views of the target square that would be obtained when approaching it from the current recall location. In two separate experiments in an outdoor urban environment, pedestrians were approached at various interview locations and asked to draw sketch maps of one of two well-known squares. Orientations of the sketch map productions depended significantly on distance and direction of the interview location from the target square, i.e. different views were recalled at different locations. Further analysis showed that location-dependent recall is related to the respective approach direction when imagining a walk from the interview location to the target square. The results are consistent with a view-based model of spatial long-term and working memories and their interplay.

Citation: Röhrich WG, Hardiess G, Mallot HA (2014) View-Based Organization and Interplay of Spatial Working and Long-Term Memories. PLoS ONE 9(11): e112793. doi:10.1371/journal.pone.0112793

Editor: Paul Graham, University of Sussex, United Kingdom

Received July 9, 2014; **Accepted** October 17, 2014; **Published** November 19, 2014

Data Availability: The authors confirm that all data underlying the findings are fully available without restriction. All relevant data are within the paper and its Supporting Information files.

Funding: This work was carried out at the Department of Biology of the University of Tübingen. WGR received additional support from the Werner Reichardt Center for Integrative Neuroscience (CIN) at the University of Tübingen. The CIN is an Excellence Cluster funded by the Deutsche Forschungsgemeinschaft (www.dfg.de) within the Excellence Initiative under grant number EXC 307. Additional support was provided by the German Federal Ministry of Education and Research (www.bmbf.de) within the Tübingen Bernstein Center for Computational Neuroscience under grant number 01GQ1002A. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

As we walk through an environment, we constantly keep track of objects, landmarks, and path opportunities around us. This environmental information forms a working memory of surrounding space for which Loomis, Klatzky, and Giudice [1] suggested the term "spatial image". Local, ego-centric representations of space have been studied in many contexts, including among others sensori-motor integration, visual scene recognition, and spatial cognition. Tatler and Land [2] and Land [3] review a large body of evidence on ego-centric visual representation supporting the stability of perception across eye-movements as well as eye-hand coordination with and without locomotion of the body. The representation considered by Tatler and Land [2] extends around the agent up to about the size of a room in an indoor environment. A similar spatial working memory including also a mechanism for spatial updating has been suggested by Byrne, Becker, and Burgess [4]. The notion of the spatial image [1] is slightly more general in that it may include knowledge from other (non-visual) modalities and extends to more distant spaces, which may be out of sight even if the observer would turn his or her head accordingly. Information from distant locations beyond the current sensory horizon can originate from two sources, i.e. long-term memory of distant places, or spatial updating if the distant place had been visited before and was since maintained in working memory.

Multiple representations of space

Multiple representations of space have been suggested for a number of reasons. One issue is the problem of scale which may vary from centimeters in manipulation tasks to thousands of kilometers in way-finding. Grüsser [5] distinguishes a (mostly metrical) grasp space, a near- and a far-distance action space, and a visual background. Montello [6] presented a classification of "psychological spaces" also based on scale, in which the spatial image discussed here is somewhere between "vista space" (what is currently visible) and "environmental space" (the area a subject is used to navigate in).

The distinction between working and long-term memories of space is grounded both in behavioral and neurophysiological data [7,8]. Spatial working memory tasks which are largely independent of spatial long-term memories include spatial sequence learning such as walking versions of the Corsi block-tabbing task [9], perspective taking and spatial updating [10], walking without vision [11], path integration [12,13], path-planning in multi-local tasks [14], etc. Interactions of spatial working and long-term memories are crucial in way-finding, i.e. the planning of novel paths from known segments [15–17], spatial imagery [18], direction giving, and other tasks. Wang and Brockmole [19] studied spatial updating, a typical working memory task, in nested environments and concluded that spatial updating acts differently on close (the surrounding room) and distant (the outdoor buildings) environments. Giudice, Klatzky, Bennett, and Loomis [20] addressed the interaction of long-term and working memories in a pointing task involving the angle between items stored in the different memory systems.

In a study by Basten, Meilinger, and Mallot [21], visitors of the University restaurant of the University of Tübingen were asked to draw sketches of the "Holzmarkt", a central and familiar downtown square about two kilometers away. Drawings were rated for orientation and a clear preference for the southward view was found, depicting a landmark church building on top of a hill. However, when subjects had been asked prior to the sketching task to imagine walking a route passing by the target square in one of two opposite directions, drawings in the respective viewing direction became significantly more frequent. The authors concluded that mental travel activated a view-dependent ("ego"-centric with respect to the imagined travel) representation of the target square which later primed the sketching process.

A particularly interesting case for the present discussion is representational neglect studied by Bisiach and Luzzatti [22], which shows that (at least in patients suffering from hemilateral neglect), recall of spatial long-term memories depends on the subject's imagined position and orientation. One obvious interpretation of this finding is that recall from long-term memory goes into some sort of spatial image, or working memory centered at the observer's imagined position and that it is the left side of this representation which is affected by neglect.

Spatial memory systems may differ in the reference system employed to organize spatial information. Perception is ego-centric and so is the assumed spatial image [1,2,23]. In perspective taking, route planning, and mental travel, ego-centric memories centered at imagined positions may also exist. The reciprocal term, allocentric, is harder to define. Summarizing discussions e.g. by Klatzky [24], Burgess [23], and Mallot and Basten [25], we define an allocentric memory as one that does not change as the observer moves. Note that this definition does not refer to coordinate systems or global anchor points. Indeed knowledge such as distances between places as well as oriented views and their relation to other oriented views qualifies as allocentric memory in this sense, because it can be carried around and remains useful without a need for movement-dependent changes or transformations. Almost as a corollary to this definition, long-term memories will always be allocentric, while working memories involving automated spatial updating will be not. In the Model section, we describe the view-graph [26] as an allocentric data structure for spatial long-term memory that lends itself easily to interactions with ego-centric working memories.

Over the past decade, imaging studies have identified an extensive network of cortical and subcortical brain areas involved in a variety of spatial behaviors. Tasks involving an interplay of spatial long-term and working memories have been shown to recruit structures such as the retrosplenial cortex as well as medial temporal lobe [27–30]. More on the visual side, scene recognition as well as imagery of out-of-sight places or perspectives has been related to various parts of the parietal cortex and transverse occipital sulcus [31–33].

A view-based model of spatial working and long-term memories

In the interplay between spatial working and long-term memories, the encoding, or data-format, used by each memory structure is of great importance. Recall from long-term memory into spatial working memory, i.e. between allocentric and ego-centric representations, is often thought to require a coordinate transform, which is certainly true if spatial information is explicitly represented in the form of coordinates. However, in a view-based account, an allocentric, long-term representation of place may even be a view or a collection of views which were egocentric when first perceived and stored, but are now carried around for reference. Simply enough, transformation of this view-based allocentric representation into an egocentric one amounts to picking a particular view which corresponds to the current viewing direction and loading this view into working memory, e.g. for comparison to the currently visible view of the present place. As a result, places would be recognized by view matching [34], similar to the snapshot algorithms discussed in insects [35]. In addition to simple matching, a process of view transformation might be involved, allowing the prediction of nearby or intermediate views from stored ones, as has been suggested for robot applications [36]. Such a mechanism seems to be required also in the pointing task studied by Giudice et al. [20], involving both long-term and working memories. In pose-invariant object recognition, view interpolation is a well-established mechanism [37,38].

The concept of view-based representations of navigational space has been developed by Schölkopf and Mallot [26] and used in robot simulations [39] and models of hippocampal processing [40]. Behavioral evidence for view-based navigation in humans has been presented by [41–43]. View specific neuronal activity has been reported e.g. from the monkey parahippocampal formation [44] or the human retrosplenial cortex [30].

The central spatial concept of the view-based framework is the view, i.e. an image or early visual representation of a sector or angle of the environment taken at a position $\mathbf{x}=(x_1,x_2)$ and with a viewing direction φ; we denote the view by $v(\mathbf{x},\varphi)$. It need not be limited by the visual perimeter, but may also contain information from beyond the current visual horizon, encoded in an egocentric way, see, for example, Tatler and Land [2]. The simplest long-term memory of a place $\mathbf{x}_o$ is then a collection of views taken at that place, $\{v(\mathbf{x}_o,\varphi_i), i=1,\ldots,n\}$ where the index i enumerates the individual viewing directions and n is the total number of views stored for the particular place (see Figure 1a). The views may be overlapping and the distribution of viewing directions φ_i may be anisotropic. If, for example, one particular view of a place is especially salient, we may model this by assuming that multiple copies of this view, or largely overlapping adjacent views, will be included in the place representation. In analogy to object representation, such views might be called "canonical" for the respective place. In addition to the views themselves, we assume that the adjacencies of views are also represented in the place code. The views together with their adjacencies thus form a simple view-graph with a ring-topology. As in [26], the adjacency links will be labelled with action codes such as "turn left", or "turn right 40 degrees".

From this place representation, a long-term memory of a larger environment, i.e. a cognitive map, can be built as a full view-graph and used for way-finding (see Figure 1b). For multiple places, interplace view adjacencies have to be stored as "action labels" representing egocentric locomotor actions such as "walk straight from here" or "follow the street from here". In these action labels, "here" refers to a view from the current place assuming the observer's current heading. The link will end at a view of a

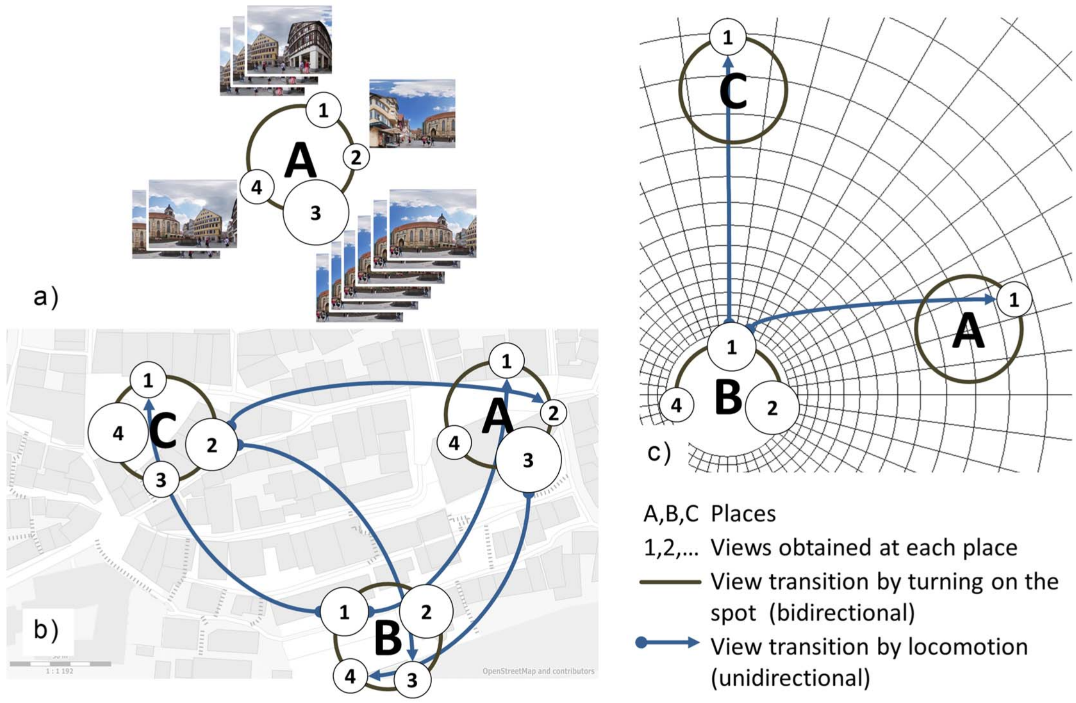

Figure 1. View-based model of spatial long-term memory. Upper case letters A, B, C denote places, numbers (1–4) denote views visible at each place. E.g., view A3 depicts a church building when standing at the ''Holzmarkt'' (A), facing south. a) Place representation composed of a collection of directional views (1–4) obtained at a place A. Views may be represented multiply, or overlapping, allowing to represent viewing direction in a population code. The size of the circles indicates the frequency with which each view is stored, or the likelihood that it is read out in recall. (Tübingen Holzmarkt icons are sections of a panoramic image retrieved with permission from www.kubische-panoramen.de.) b) View-graph of 12 views (A1-C4) belonging to three places. Within each place, views are linked by turning movements. Views of different places are linked by movements involving translations. Note that these links are unidirectional; for example a path from A to B starts from view A3, while the return from B to A will end on A1. c) A view-based model of spatial working memory is obtained by extracting a sub-graph from the total view-graph. It contains the current view (B1) which also marks the current observer position and forward direction, and its outward neighborhood of order 1, i.e., the directly adjacent views (A1, B2, B4, C1). Outward neighborhoods of higher orders may also be represented but are not shown in the figure. The polar grid is added to indicate that metric updating may take place in the working memory, which, however, does not play a role in the experiment reported in this paper. Map source: © OpenStreetMap contributors.
doi:10.1371/journal.pone.0112793.g001

neighboring place, as it appears when arriving from the starting location. As was demonstrated by Schölkopf and Mallot [26], the resulting view graph contains sufficient information for route planning between connected views.

As a model of spatial working memory, we suggest a sub-graph of the full view-graph, consisting of the current view corresponding to the observer's current position and orientation, and the views reachable from this current view in a small number of steps s, i.e. the outward neighborhood $N_s(v_o)$. Note that the graph links are directed, allowing to distinguish an outward neighborhood (views reachable from v_o) from an inward neighborhood (views from which v_o can be reached). In Figure 1c, we show the one-step ($s=1$) outward neighborhood of view 1 of place B. As the observer moves, the current view will change and so will its outward neighborhood represented in working memory. This may be achieved by repeatedly refreshing the neighborhood from long-term memory, i.e. loading the appropriate sub-graph after each movement step. Alternatively, or on smaller scales, one could think of some sort of ego-motion driven image transformation (spatial updating) within working memory. We indicate this possibility by adding a polar coordinate grid to working memory in Figure 1c. In our experiment, we cannot distinguish between refreshing from long-term memory and spatial updating within working memory. See [20] for an experiment directly addressing this problem.

When asked to imagine a nearby target place $\mathbf{x}_t$, subjects will recall from memory one of the stored views $v(\mathbf{x}_t,\varphi_j)$ of this place. In spatial working memory, only the views contained in the outward neighborhood of v_o will be present. Therefore, if recall is based on working memory content, the view obtained when (mentally) traveling from the current ''here'' to the target place will be selected. In this case, we predict that in visual recall of a target place, the recalled viewing direction will depend on interview location. If, however, recall is based solely on long-term memory, one of the known views of the target place will be selected independent of interview location.

For the analysis of the data presented below, we introduce the following notation: Let $p_{i,t}(\varphi)$ denote the probability that the recalled view of target place $\mathbf{x}_t$ has the orientation φ, given that the interview location is $\mathbf{x}_i$. Let further $L_t(\varphi)$ and $W_{i,t}(\varphi)$ denote the probability densities of recalling a view φ if recall is from long-term or working memory, respectively. Note that the working memory contribution depends on interview location, whereas the long-term memory contribution does not. We expect that $W_{i,t}(\varphi)$ is a peaked distribution with a maximum at the approach direction from interview location $\mathbf{x}_i$ to target place $\mathbf{x}_t$. In the data analysis, we will identify the approach direction with the air-line direction between the two places,

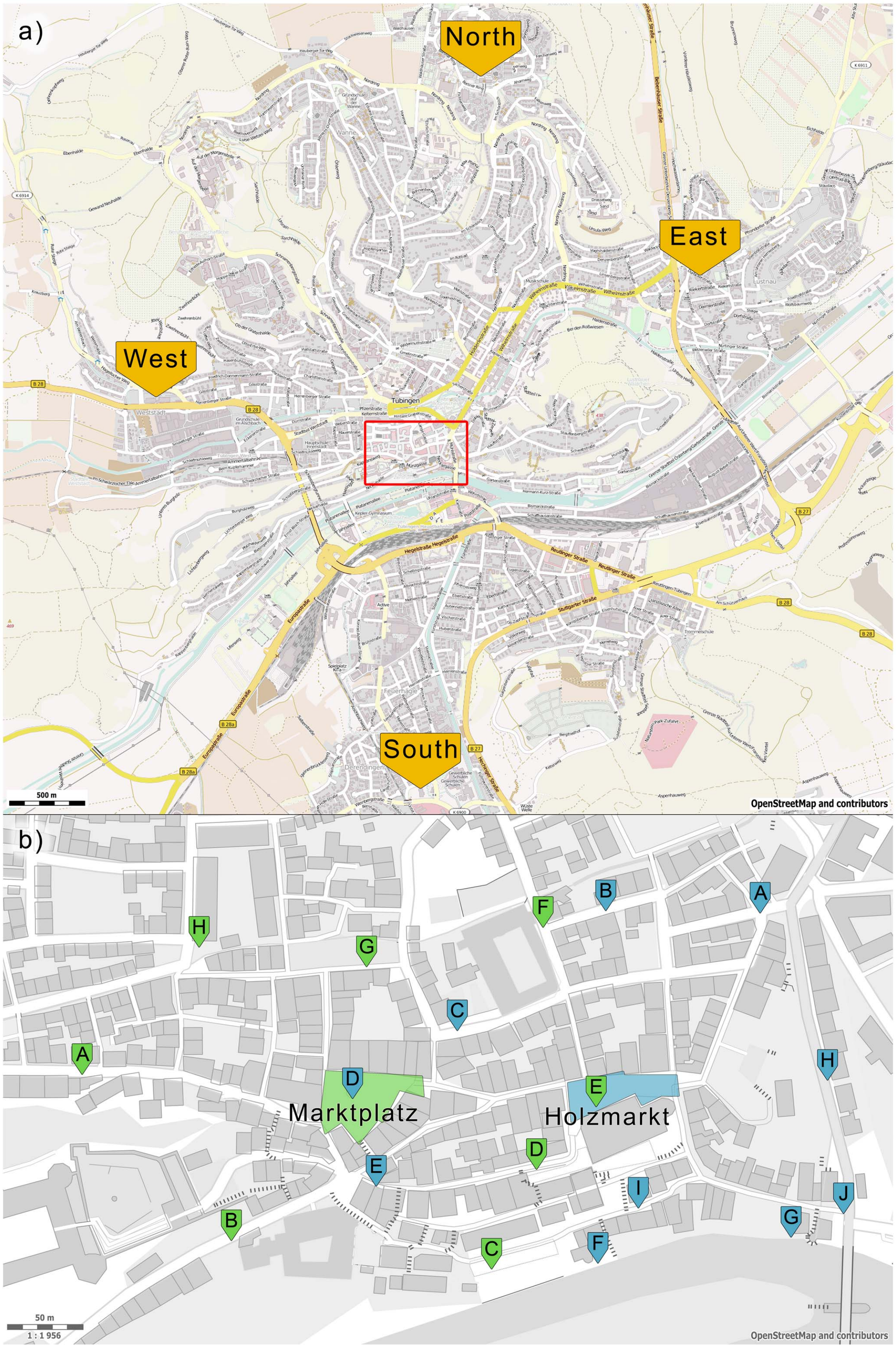

Figure 2. City maps of Tübingen with interview locations and target places (''Holzmarkt'' & ''Marktplatz''). a) Distant (suburban) interview locations (North, East, South, West) were located in small shopping areas about 2 km away from the target squares, which were inside the downtown area (red square). b) Close-up view of the downtown area of Tübingen. Blue: Interview locations (A–J) and target place for experiment 1 (''Holzmarkt''). Green: Interview locations (A–H) and target place for experiment 2 (''Marktplatz''). Map source: © OpenStreetMap contributors.
doi:10.1371/journal.pone.0112793.g002

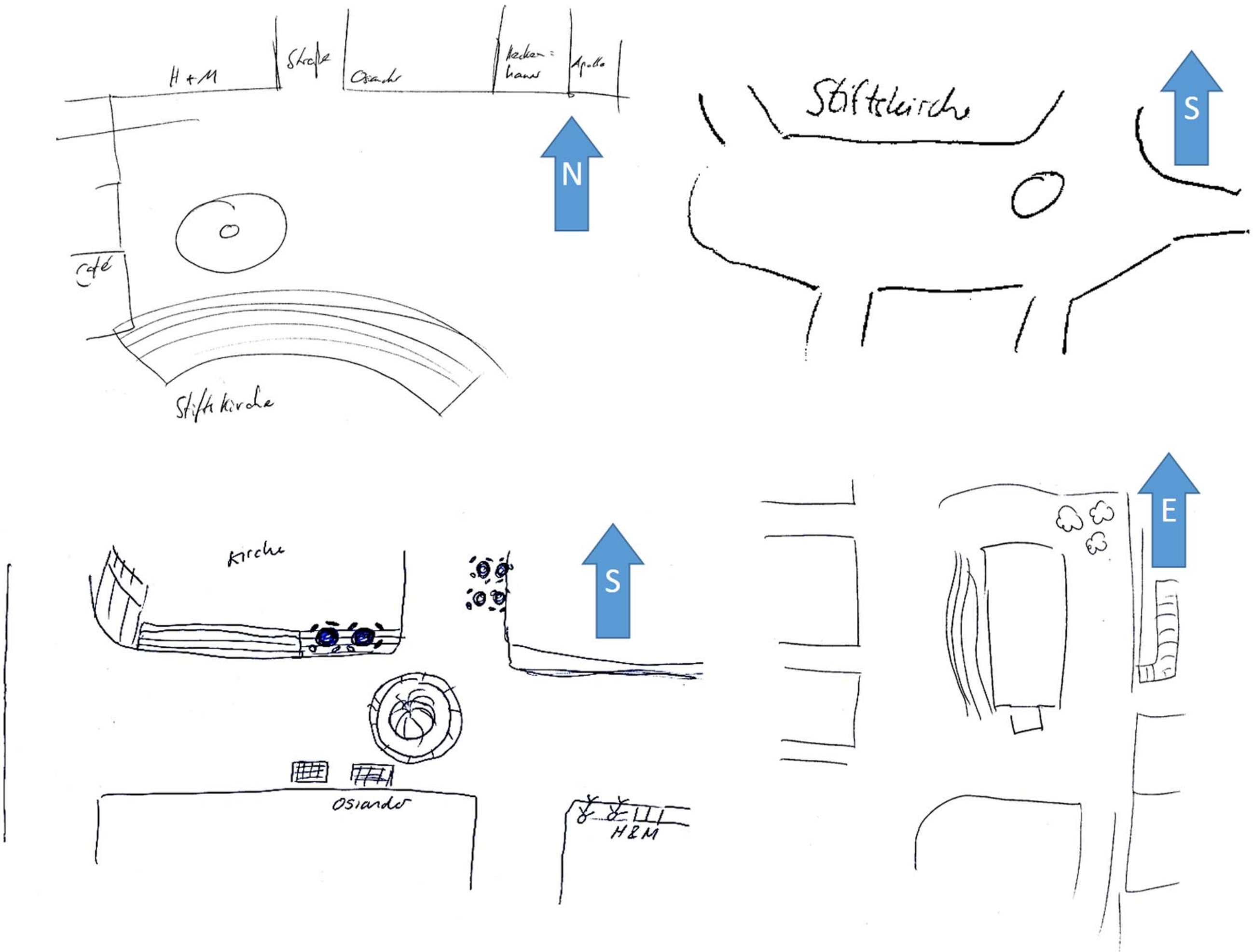

Figure 3. Examples of sketches of the "Holzmarkt" from four participants. The blue arrows indicate the orientation the sketch was rated in. Note the inscriptions "Stiftskirche" or "Kirche" referring to the landmark church building located at this square (see also view A3 in Figure 1a). The parallel lines mark a flight of stairs leading from the square to the church, the circles mark a fountain at the Western side of the square.
doi:10.1371/journal.pone.0112793.g003

$$\varphi_{i,t} = \operatorname{atan2}(\mathbf{x}_t - \mathbf{x}_i), \tag{1}$$

where atan2 is the inverse tangent function with two arguments. For the distribution of the recalled view orientations, we obtain

$$p_{i,t}(\varphi) = \alpha L_t(\varphi) + (1-\alpha) W_{i,t}(\varphi), \tag{2}$$

where $L_t(\varphi)$ and $W_{i,t}(\varphi)$ and are the long-term and working memory contributions, respectively and α is a mixing factor varying between 0 and 1. It reflects the relative strength of long-term and working memory components in the recall. We expect that α is less than 1 for interview sites close to the target place and 1 for distant interview locations.

If, for a given target place, the interview locations are spaced regularly around this place, the average of the $W_{i,t}(\varphi)$ will approach the uniform distribution, $(1/n)\sum_{i=1}^{n} W_{i,t}(\varphi) \approx 1/2\pi$ and we may estimate the long-term memory contributions as

$$\alpha L_t(\varphi) \approx \bar{p}_{\cdot,t} - \frac{1-\alpha}{2\pi}, \tag{3}$$

where $\bar{p}_{\cdot,t}(\varphi)$ denotes the average view distribution over all interview locations. From this, we will calculate an estimate for the working memory contribution as

$$W_{i,t}(\varphi) \propto p_{i,t}(\varphi) - \bar{p}_{\cdot,t}(\varphi) + c, \tag{4}$$

where c is a constant reflecting the non-zero average of the working memory distributions. In the analysis of the experimental data, orientations are sampled to the four cardinal directions (N, E, S, W). The constant c cancels out in the calculation of the circular vectors following Equation 5 below. In analyses of the distribution $W_{i,t}(\varphi)$ this constant is important to avoid negative values; it can be set to 0.25. The proportionality factor in Equation 4 will be ignored in the sequel.

Experiment 1 – "Holzmarkt"

Material and Methods

Passers-by at 14 locations in Tübingen (see below and Figure 2) where approached during day time and asked "if they would participate in a quick interview for a navigational study". They were informed about the type of the collected data and the general

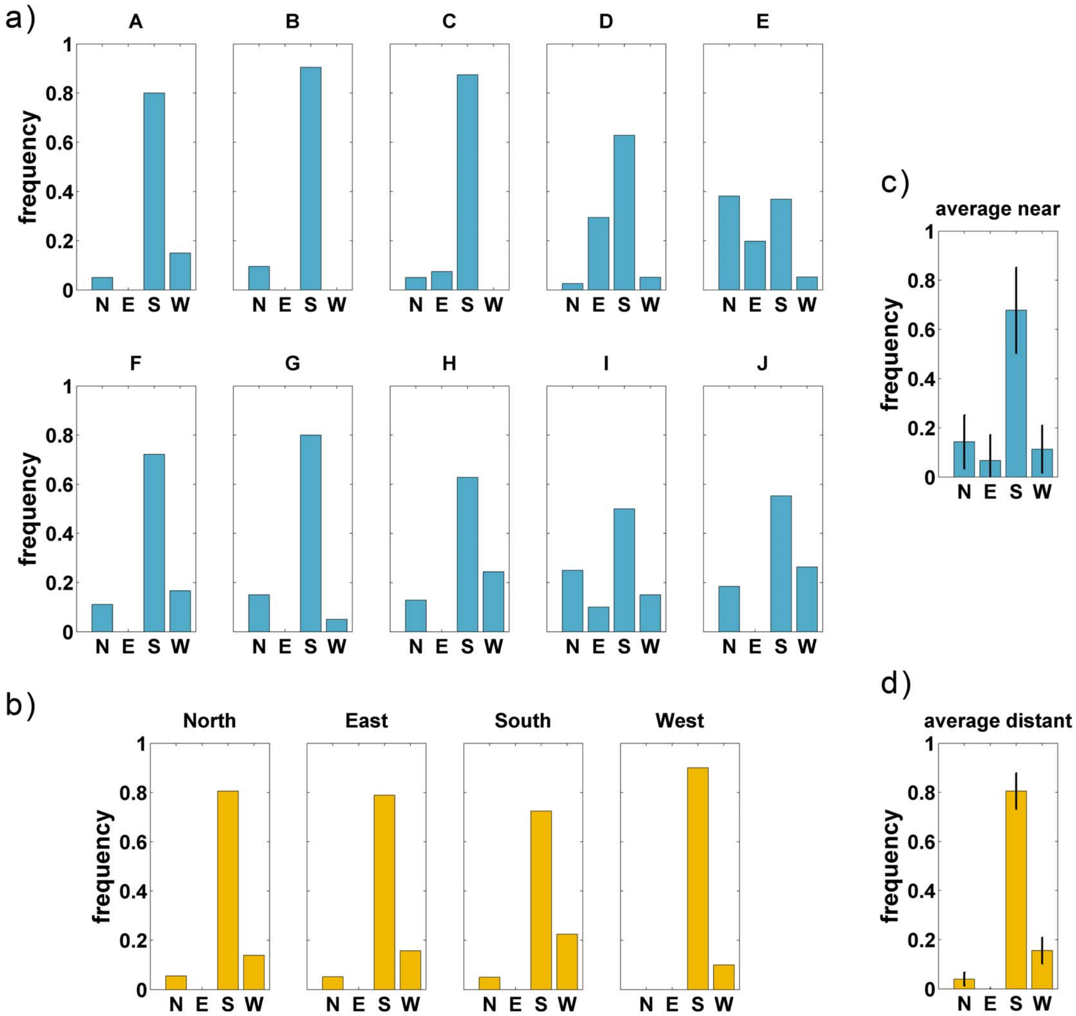

Figure 4. Sketch orientation frequencies for drawing the ''Holzmarkt''. a) Orientation frequencies of the near interview locations (A–J). The obtained frequencies differed significantly from each other. b) Orientation frequencies of the distant interview locations (North to West). c, d) Average orientation frequencies with standard deviation of the near and distant condition, respectively. The y-axis shows the frequency of sketch map orientations, the x-axis the rated orientation (North, East, South, West).
doi:10.1371/journal.pone.0112793.g004

procedure. About one third agreed to participate (verbal informed consent) as was documented by their later participation in the interview. Participants were not asked for their names and accordingly were not required to give their consent in writing. Participants were free to terminate their participation at any time, simply by walking away. The informed consent procedures adheres to the guidelines of the Declaration of Helsinki, approval by the local ethics committee was not required.

Participants were requested to ''sketch the layout of the Holzmarkt'' (timber market), a well-known down-town square, on an A4 sheet of paper. After sketching, they were asked for their age, years of residency in Tübingen, own judgment of general navigation skills, and own judgment of local knowledge (see below). Only sketches by subjects who had lived in Tübingen for more than two years were analyzed further. In total, these were 335 adults (161 male, 174 female). An interview and sketch map production took less than two minutes in total. Examples of sketch maps appear in Figure 3.

Interviews took place outdoors, either at one of four distant locations in small suburban shopping areas about 2 km away from the target square (''distant'' condition) or at one of ten downtown locations in walking distance (about 150 m) to but out of sight of the target square ''Holzmarkt'' (''near'' condition; see Figure 3). Care was taken to approach participants walking in different directions. Approach was from sideways with respect to the participant's heading. Upon being approached, participants stopped but did not change their general body orientation. Also during recall, no regular turning movements of the participants were observed.

The sketches were categorized for orientation (North, East, South or West up) by three independent raters. From the 335 drawings 331 were judged identically (99%) with a chance-corrected inter-rater reliability of $\kappa = 0.98$. A small number of sketches was consistently rated diagonal; in these cases, the number 0.5 was added to the two adjacent directions. Only the 331 identically judged drawings were analyzed further (254 near condition, 77 distant condition). The mean age of the 331 participants whose maps were included was 33.36 years, their average time of residency in Tübingen was 12.9 years, their own judgment of local knowledge and general navigation skills was 5.9 and 6.2, respectively, both on a scale between 1 and 9 with 1 = very poor and 9 = very good.

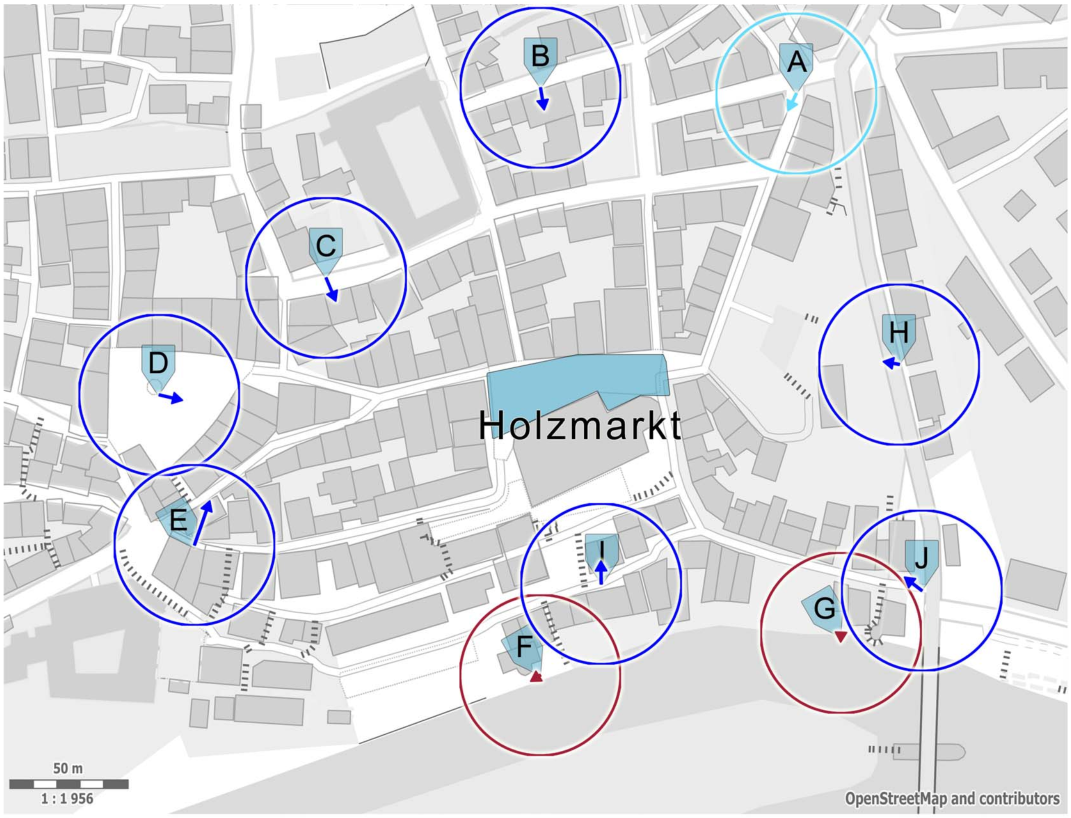

Figure 5. Downtown map of Tübingen with interview locations (A–J) for the near condition and target square ''Holzmarkt''. The vectors show the average sketch map orientation at the respective interview site. At seven (blue circles) out of ten near sites sketch orientations were found to point from the interview location in the direction of the target square ($p < 0.05$ or better). At one location, a strong tendency was indicated (A, cyan, $p = 0.051$). For two locations (F,G; red), no significant orientation effect could be found. Vector length ranges from zero to one (radius of circle) and is a measure of concentration of the location-dependent vectors. Map source: © Open-StreetMap contributors.
doi:10.1371/journal.pone.0112793.g005

For each interview location i, relative frequencies of ratings for the four cardinal directions were calculated and denoted as (n_i, e_i, s_i, w_i) for North, East, South, and West. Average frequencies were also calculated separately of the ten ''near'' and the four ''distant'' interview locations and denoted as $(\bar{n}_i, \bar{e}_i, \bar{s}_i, \bar{w}_i)$. In the next step, the average frequencies from the ''near'' interview locations were subtracted from each of the local histograms of the ''near'' condition. Similarly, the average frequencies for the four distant interview locations were subtracted from the distant histograms. We refer to the results as the ''location-dependent components'' and consider them as an estimator of local working memory content, according to Equation 4. Finally, these location-depenedent components were transformed into location-dependent orientation vectors

$$\mathbf{w}_i = \begin{pmatrix} (e_i - \bar{e}) & - & (w_i - \bar{w}) \\ (n_i - \bar{n}) & - & (s_i - \bar{s}) \end{pmatrix}. \tag{5}$$

The orientation of these vectors is an estimator of the circular mean of the working memory distribution $W_{i,t}(\varphi)$ from Equation 4. The length is a measure of concentration of this distribution related to the circular variance [45,46]. A long vector means more concentration (more coherent sketch orientations) and stronger differences from the average (long-term memory) distribution. Short vectors would result from sketch orientations that are similar to the long-term memory content.

Results

Orientation frequencies of the sketches of the ten downtown and four suburban interview locations are shown in Figure 4; for the orientation counts, see Figure S1. The distributions obtained at the near locations differ significantly from each other ($\chi^2(27, N = 254) = 88.036; p < 0.001$) indicating that recalled view orientation depends on interview location. For the distant locations, no differences between the histograms could be found.

The average distributions for near and distant interview sites are shown separately in Figure 4. These distributions are significantly different from each other ($\chi^2(3, N = 331) = 12.654; p < 0.01$) though comparable in shape.

The orientation vectors obtained from the location-dependent components of the downtown interview locations (Equation 5) are plotted in Figure 5 superimposed on a map of Tübingen showing the target and interview locations. An overall tendency of the vectors to point to the target square is clearly apparent.

In order to test this tendency, we calculated the angular deviation between the location dependent orientation vectors and the theoretical air-line vector obtained for each interview location by subtracting the coordinates of the target square (defined as the center of gravity of the blue area in Figure 5) from the coordinates of the interview sites (Equation 1). For each interview location, the deviation or bias of the data from a uniform distribution towards the theoretical direction was tested with the circular V-test [45,46], taking into account the vector length as a measure of concentration. The deviations towards the theoretical direction are

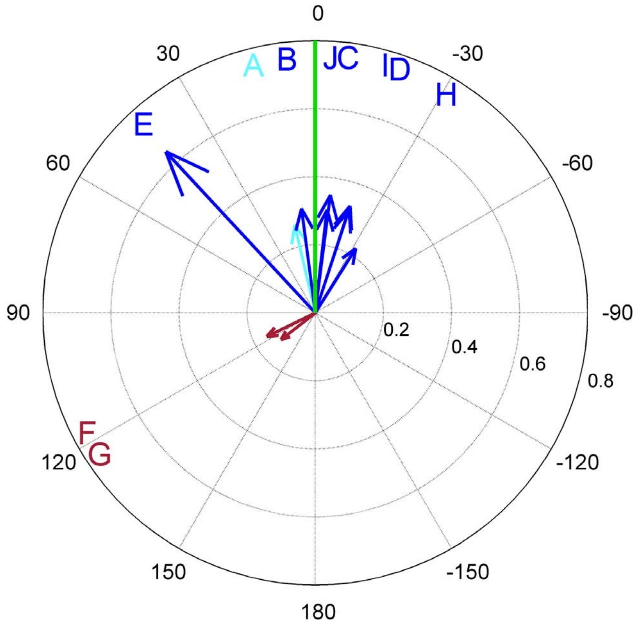

Figure 6. Location-dependent vectors from Fig. 5, rotated to align the air-line directions from all interview locations to 0 degrees (letters indicate interview locations). Vectors are significantly biased towards the theoretical direction (green line, $p<0.001$). Vector length reaches from zero to one (radius of circle) and is a measure of concentration of the location-dependent vectors.
doi:10.1371/journal.pone.0112793.g006

significant ($p<0.05$ or better) for seven out of ten interview locations, and marginally significant for an additional one ($p=0.051$). For two interview locations (F and G in Figure 5), no significant deviation from uniformity could be demonstrated.

Figure 6 shows the location-dependent vectors rotated such that the theoretical direction for each interview location appears in upwards direction. For this sample of 10 vectors, we again applied the circular V-test, this time with the 0-degree-vector as a theoretical direction. For the overall sample, bias towards the theoretical direction was significant with ($V(N=254)=0.234; u=5.276; p<0.001$).

For the four distant interview locations no such orientation effect could be found ($V(N=77)=0.038; u=0.477; p=0.317$).

Experiment 2 – "Marktplatz"

To test the robustness of the findings of the first experiment with respect to other target squares, we chose another well-known square and repeated the previous experiment.

Material and Methods

Eight new interview locations around the "Marktplatz" (market square) were selected for the near condition (Figure 2b, green). For the distant condition the same locations as in experiment 1 were used except for the southern one, which we did not again get access to. 330 passers-by agreed to participate. The procedure was the same as in experiment 1.

Sketches were again categorized for orientation (North, East, South or West up) by three independent raters. From the 330 drawings 306 were judged identically (93%) with a chance-corrected inter-rater reliability of $\kappa=0.93$. Only the 306 identically judged drawings were analyzed further (220 near condition, 86 distant condition). The mean age of the 306 participants (131 male, 175 female) whose maps were included was 37.4 years, their average years of residency in Tübingen was 12.7, their own judgment of local knowledge was 3.4 (with 1= very poor and 9= very good) and own judgment of how often they frequent the "Marktplatz" was 3.0, with 1= very rarely and 9= very often.

Average orientation frequencies for the near and distant conditions were calculated and subtracted from the histogram of the near and distant interview locations, respectively, yielding the location-dependent components of each distribution.

Results

Orientation frequencies of the sketches of the eight near interview locations differed significantly from each other ($\chi^2(21,N=220)=95.457; p<0.001$). For the distant locations, no difference between the histograms could be found (Figure 7). Also, there was no significant difference between the near and distant average frequencies ($\chi^2(3,N=306)=3.986; p=0.263$).

As shown in Figure 8, the majority of the location-dependent vectors of the near condition point towards the "Marktplatz" (center of gravity of green area in Figure 8). A significant bias of sketch orientations towards the air-line direction to the target square (center of gravity of the green area Figure 8) for six of the eight interview locations could be revealed by a circular V-test. The sample of eight location-dependent vectors, rotated to align their respective air-line directions, also showed a highly significant bias towards the theoretical direction at zero degrees ($V(N=220)=0.343; u=7.203; p<0.001$) (Figure 9).

No bias could be detected for the three distant interview locations ($V(N=86)=0.099; u=1.295; p=0.098$).

Discussion

The data presented in this study indicate that visuo-spatial recall of out-of-sight places does not occur with a random or fixed orientation but that recall orientation depends on both target and interview location.

The target square effect suggests a non-isotropic representation of each target square in long-term memory. For the distant (suburban) interview locations, orientation distributions were found that equal the average distributions taken over all near (downtown) locations. We therefore conclude that the target square dependence is underlying all our measurements and is modulated by interview location-dependent effects visible only for the downtown interview locations. The average view distribution for the "Holzmarkt" square (Exp. 1) is strongly peaked with a "canonical view" in southward direction, depicting a landmark church building on top of a hillock. In contrast, the view distribution for the "Marktplatz" (Exp. 2) is more isotropic, probably reflecting the more balanced salience of the surrounding houses. These differences are probably related to the specific topography of each place. The "Holzmarkt" is rising to the South, with a prominent church building on top. Approaches from behind the church (Northwards) are almost impossible and very rarely walked. Drawings with the church on top might thus be favored by familiarity, alignment with environmental axes and the fact that uphill buildings will appear on top of the sketching paper. In contrast, the salience of the buildings surrounding the "Marktplatz" (Exp. 2) is much more balanced. The "Marktplatz" is also rising to the South, but the most prominent building, the city hall, appears not on top but on the Western side. Also, approaches from all directions are possible and frequently walked. Still, a peak in the experimental data towards "South" and "West" is apparent here, too. We suggest that the long-term memory of

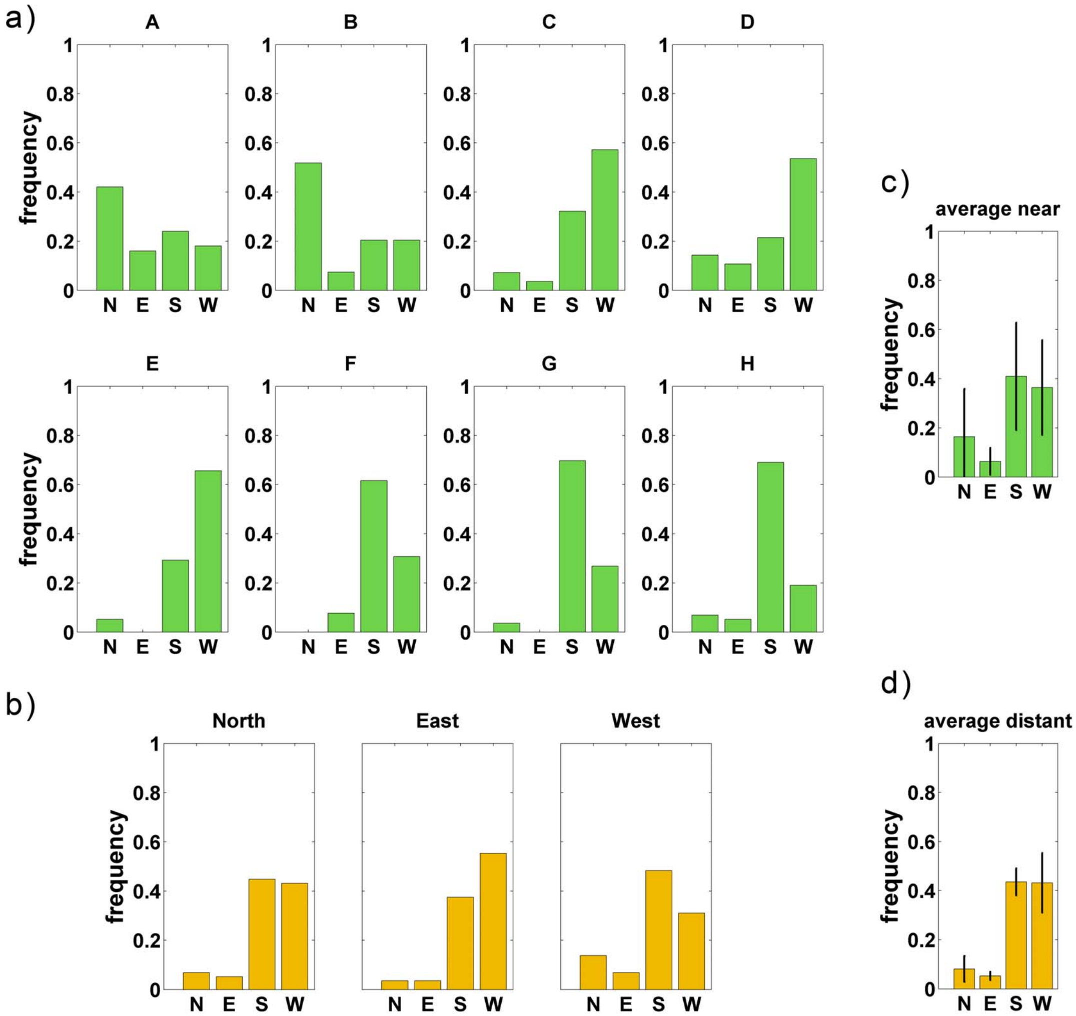

Figure 7. Sketch orientation frequencies for drawing the ''Marktplatz''. a) Orientation frequencies of the near interview locations (A–H). The obtained frequencies differed significantly from each other. b) Orientation frequencies of the distant interview locations (North, East and West). No significant difference could be found. c, d) Average orientation frequencies with standard deviation of the near and distant condition, respectively. The y-axis shows the frequency of sketch map orientations, the x-axis the rated orientation (North, East, South, West).
doi:10.1371/journal.pone.0112793.g007

either square is organized as a collection of discrete views (Figure 1a), sampling the various viewing directions with variable resolution much as has been suggested for view-dependence in face recognition [37]. Allocentric place memory might therefore be organized as a population code of orientation-specific memories. Indeed, neuronal specificities for views of places have been reported in the medial temporal lobe, see for example [47,48].

The formation of one or several canonical views of a place requires further study, concerning potential relationships to canonical views of landmark objects and the selection of one view or another as canonical. Reasons for selection might include: Distinctiveness to other places, availability and distribution of local landmarks, geometric layout, visual salience of objects, path options and functionality, or intrinsic axes of the environment [49].

The distribution of recalled views depends also on interview location as was revealed by Chi-Squared tests on the orientation histograms. For the near (downtown) interview locations each local distribution is biased towards a preferred orientation roughly corresponding to the air-line direction from the interview location to the target square. A view of the target square, oriented in the current approach direction, thus seems to be activated in a spatial working memory either by automated spatial updating when walking in the city, or by a mental travel initiated when asked to draw the sketch, or by both effects (see Figure 1b,c). Spatial updating itself could again be achieved by two mechanisms, either image transformation as discussed in view-based object recognition [38] or by refreshing working memory from long-term memory.

In the introduction, we presented a view-based model of spatial recall predicting that the directional distributions of recalled sketch maps are a mixture of a fixed long-term memory distribution and a set of position dependent working memory distributions (Equation 3). As a direct test of this model, we performed a maximum likelihood analysis assuming for the orientation histograms a multinomial distribution with four possible outcomes (N, E, S, W) and theoretical probabilities $\alpha l_k + (1-\alpha) w_{ik}$, where k numbers the four possible outcomes and $(l_1, \ldots, l_4)$ are the class averages over all interview locations, i.e. the assumed long-term memory contributions. The log likelihood function reads

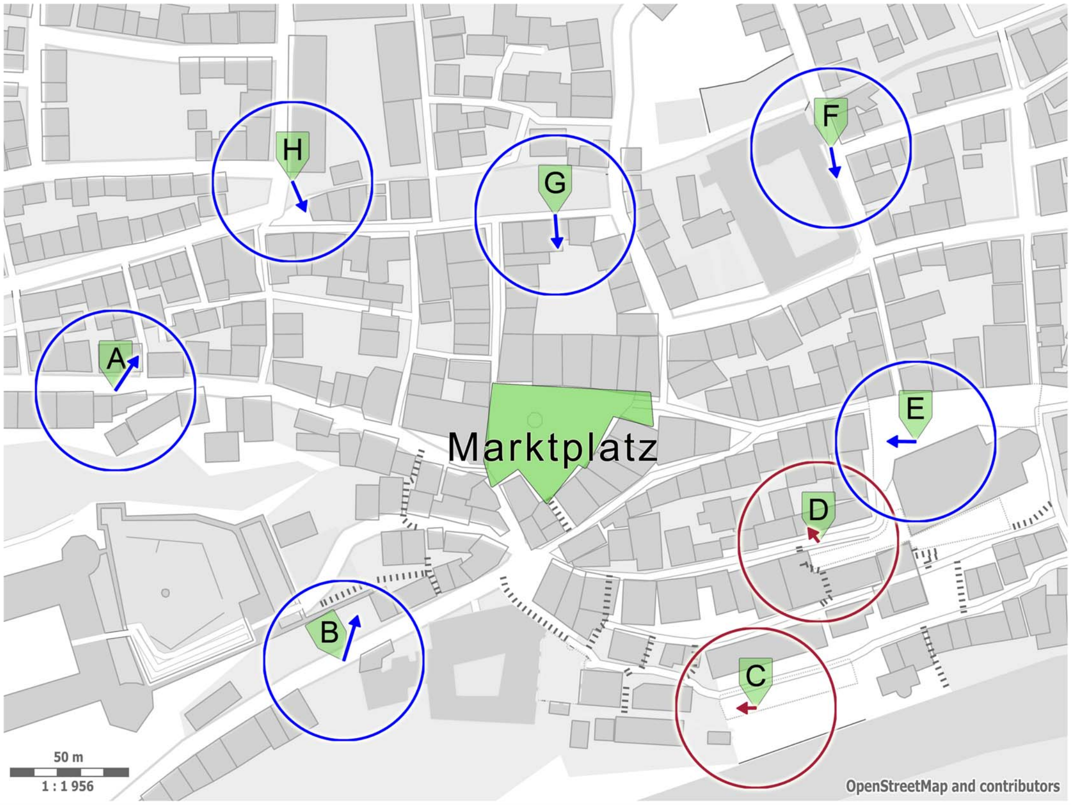

Figure 8. Downtown map of Tübingen with target square ''Marktplatz'', near interview locations (A–H) and location-dependent vectors drawn at these locations. Vectors at six (blue circles) out of eight interview sites point towards the target square ($p < 0.05$ or better). For two locations (C, D; red), no significant orientation effect could be found. Vector length reaches from zero to one (radius of circle) and is a measure of concentration of the location-dependent vectors. Map source: © OpenStreetMap contributors.
doi:10.1371/journal.pone.0112793.g008

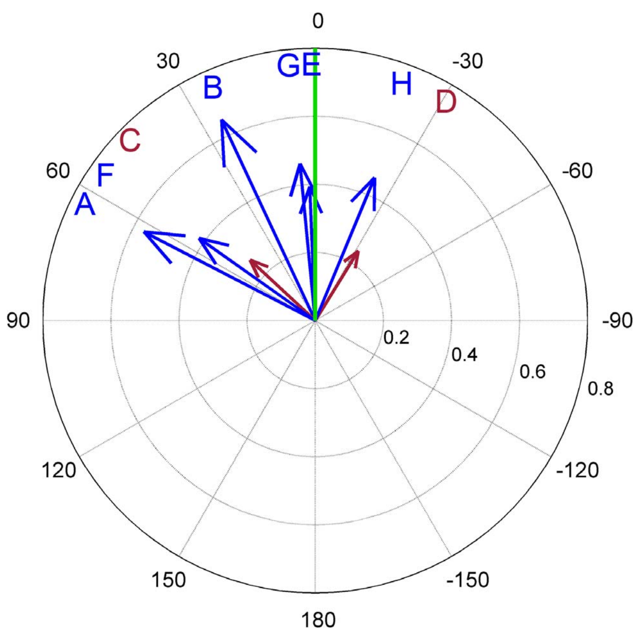

Figure 9. Location-dependent vectors from Fig. 8, rotated to align the air-line directions from all interview locations to 0 degrees (letters indicate interview location). Vectors are significantly biased towards the theoretical direction (green line, $p < 0.001$). Vector length reaches from zero to one (radius of circle) and is a measure of concentration of the location-dependent vectors.
doi:10.1371/journal.pone.0112793.g009

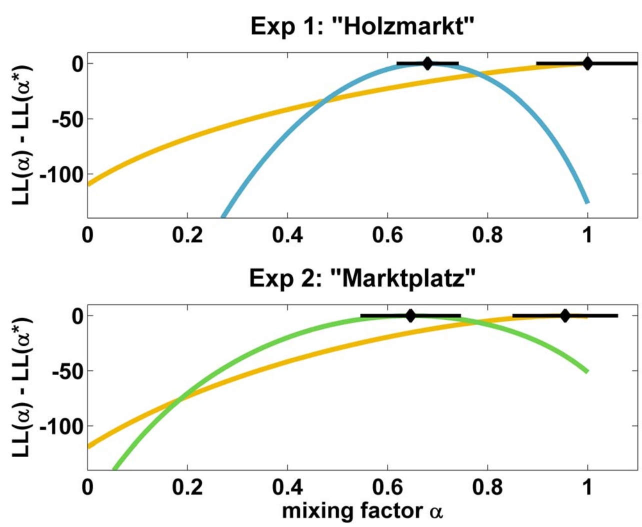

Figure 10. Likelihood analysis of the mixing model. Yellow: Distant locations, relative likelihood peaks for $\alpha^* = 1$, indicating that orientation distributions do not depend on air-line direction. Blue and green: Near locations, relative likelihood peaks at $\alpha^* < 1$, indicating the orientation distributions do depend on air-line direction in this condition. The black markers indicate with α^* with 99% confidence intervals. The y-axis shows the relative log likelihood $LL(\alpha) - LL(\alpha^*)$, the x-axis the mixing factor for working and long-term memory contributions.
doi:10.1371/journal.pone.0112793.g010

$$LL(\alpha)=\sum_{i=1}^{I}(c_i\sum_{k=1}^{4}n_{ik}\log(\alpha l_k+(1-\alpha)w_{ik})), \qquad (6)$$

where n_{ik} is the number of orientations k found at interview location i and the constant c_i is the log of the multinomial coefficient for the local orientation distribution. Theoretical estimates for the working memory contributions at each interview location are derived from the local air-line directions φ_i (Equation 1). The theoretical outcome probabilities for the assumed working memory distributions were set to $w_{i1}=c+0.5\max(0,\sin\varphi_i)$, $w_{i2}=c+0.5\max(0,\cos\varphi_i)$, $w_{i3}=c+0.5\max(0,-\sin\varphi_i)$, and $w_{i4}=c+0.5\max(0,-\cos\varphi_i)$, where $c=1-0.5(|\sin\varphi_i|+|\cos\varphi_i|)$ is a constant assuring that the four probabilities will add to 1. This distribution has the circular mean φ_i and variance 0.5, which reasonably approximates the location-dependent components shown in Figures 5 and 8.

Figure 10 shows the relative log likelihood $LL(\alpha)-LL(\alpha^*)$ as a function of the mixing parameter α separately for the near and far interview locations in both experiments. For the "far" cases, the maximum likelihood estimator α^* is 1, i.e. adding position-dependent working memory contributions to the model does not improve likelihood in these cases. In contrast, for the "near" cases, the maximum likelihood estimates lie between 0.6 and 0.7; the horizontal lines in the plot are 99% confidence intervals. A likelihood ratio test for $\alpha=1$ vs. $\alpha<1$ is significant with $p<10^{-16}$ for the "near" cases in either experiment. The model with the location-dependent working memory component thus significantly improves the fit of the data.

We cannot decide from our data whether recall bias is strictly toward the air-line direction or toward the actual entry view obtained when walking to the target place along the street network, although in a view-based account, the latter seems more plausible. Indeed, this might have been the problem with the interview location D in experiment 2 from which two roughly equidistant routes to the target place exist, each with opposite entry directions into the target square.

No location-dependent effect was found for the distant (suburban) interview locations. We conclude that in these cases, recall did not depend on working memory processes such as spatial updating or mental travel. Of course, other working memory effects might still be involved. Since we used only two distance conditions, downtown and suburban, we cannot decide how far the location-dependent effect extends around the target place or if there is a gradual decay as could be modelled by a distance-dependent factor α in Equation 2. It is clear, however, that the effect extends over tens to hundreds of meters which seem to be included in spatial working memory.

Another parameter in addition to the mere distance could be regionalization and spatial hierarchies. In virtual environments, navigators were shown to prefer routes that cross fewer region boundaries over equidistant routes through multiple regions [17]. In this experiment, regions were defined by the semantic class of landmark objects. In a pointing experiment, Wang and Brockmole [50] demonstrate that information from nested environments may be kept separate in spatial representations. In the city environments used in the present study, there are various configurations of buildings, roads, shops, etc. which segregate the environment into quarters, districts, neighborhoods, etc. Therefore it seems possible that the extension of spatial working memory is defined by region boundaries rather than by metric distance. This might also explain the results for the interview locations F and G in experiment 1 and C in experiment 2: They were probably attributed to the region "riverfront" and not "downtown", and therefore no or only weak connections to the target places existed while the experiment took place.

The theoretical account presented in the Introduction is clearly able to explain our data. In addition, the findings by Basten et al. [21] on view-based priming of recall by mental travel also fit into the overall scheme. In this study, all interviews were carried out at a distant location (the North location in Fig. 3b) and simple recall of the "Holzmarkt" square revealed the same view preference reported here. Mental travel across the "Holzmarkt", however, primed view-specific recall in the direction of travel, indicating that mental travel, just as actual walking in downtown Tübingen, activates view-specific working memories.

Alternative models of spatial working memory not based on views but on object representations and maps have been presented by [1,2,4]. While our data do not strictly rule out these models, they make clear that representations of places are not unique entities that are always activated in their entirety, but that parts of place representations can play independent roles in spatial recall. Such parts are oriented and have therefore been referred to as "views" in this paper. Alternatively, such parts could be landmarks or houses located at one side of a square, or names or other properties of such landmarks or houses, as might have been the case in the experiments reported by Bisiach and Luzzatti [22]. The considered parts of place representations are view-like in two respects: First, the target square effect (canonical view) shows that oriented parts of a place representation can be anisotropically distributed. Second, priming by spatial nearness activates oriented parts of the representation of places, not place representations in their entirety. This finding is in line with previous results of [41] who showed that associative landmark usage depends on oriented parts of place representations rather than on representations of entire places. Overall, we suggest that oriented "views" form a separate level of granularity in spatial representation that can be activated whenever view-specific information is required.

Supporting Information

Figure S1 Sketch orientation counts. The figure shows the counts for the sketch orientations for all interview locations and both experiments as determined by the rating process. In rare cases, where all raters agreed that the orientation was between two cardinal directions (e.g., SW), a count of 0.5 was added to each of the adjacent cardinal directns (e.g., S and W). The rightmost column of the table shows the airline directions from interview location to goal, computed according to Equation 1.
(XLS)

Acknowledgments

This work was carried out at the Department of Biology of the University of Tübingen. WGR received additional support from the Werner Reichardt Center for Integrative Neuroscience (CIN) at the University of Tübingen. The CIN is an Excellence Cluster funded by the Deutsche Forschungsgemeinschaft (www.dfg.de) within the Excellence Initiative under grant number EXC 307. Additional support was provided by the German Federal Ministry of Education and Research (www.bmbf.de) within the Tübingen Bernstein Center for Computational Neuroscience under grant number 01GQ1002A. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

We are grateful to Niklas Binder and Julia Mayer for help with the collection and analysis of the data.

Author Contributions

Conceived and designed the experiments: WGR GH HAM. Performed the experiments: WGR. Analyzed the data: WGR HAM. Wrote the paper: WGR GH HAM.

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8 Publication list (chronological)

8.1 Articles in peer-reviewed journals

1) Papageorgiou E., Hardiess G., Schaeffel F., Wiethölter H., Karnath H.O., Mallot H.A., Schönfisch B. & Schiefer U. (2007). Assessment of vision-related quality of life in patients with homonymous visual field defects. *Graefe's Archive for Clinical and Experimental Ophthalmology*. 245, 1749-1758.

2) Hardiess G., Gillner S. & Mallot H.A. (2008). Head and eye movements and the role of memory limitations in a visual search paradigm. *Journal of Vision*. 8(1):7, 1-13.

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12) Hardiess G. & Mallot H.A. (under revision). Allocation of cognitive resources in comparative visual search - individual and task dependent effects. *Vision Research.*

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8.2 Book chapters

1) Hardiess G., Meilinger T. & Mallot H.A. (2012). Virtual Reality and Spatial Cognition. In: *International Encyclopedia of Social & Behavioral Sciences 2nd Edition*. James D. Wright (Ed).

8.3 Conference presentations

1) Hardiess G., Gillner S. & Mallot H.A. (2005). Gaze behavior in a comparative visual search task. BIP (International Workshop on Bioinspired Information Processing, 2005)

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19) Hardiess G. & Mallot H.A. (2014). Acquisition vs. memorization trade-offs: individualized and adapted to task constraints. 56th Conference of Experimental Psychologists (Tagung experimentell arbeitender Psychologen, TeaP Giessen, March 2014).

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21) Mallot H.A., Röhrich W. & Hardiess G. (2014). A view-based account of spatial working and long-term memories: Model and predictions. Proceedings of KogWis 2014 (12th Biannual conference of the German cognitive science society). Cogn. Process. (2014), 15 (Suppl 1):S120-S123.

22) Schick W., Halfmann M., Hardiess G. & Mallot H.A. (2014). Language cues in the formation of hierarchical representation of space. Proceedings of KogWis 2014

(12th Biannual conference of the German cognitive science society). Cogn. Process. (2014), 15 (Suppl 1):S63-S64.

23) Hardiess G., Halfmann M. & Mallot H.A. (2014). Explicit place-labeling supports spatial knowledge in survey, but not in route navigation. Proceedings of KogWis 2014 (12th Biannual conference of the German cognitive science society). Cogn. Process. (2014), 15 (Suppl 1):S44.

9 Curriculum vitae

Personal information

Name	Dr. Gregor Hardiess
Home Address	Pfrondorfer Str. 2, 72074 Tübingen
Birthday & -Place:	27.11.1975 in Erfurt (Germany - Thuringia)
Nationality	german
Parents	Father: Reinhardt Hardieß; Mother: Karin Hardieß

Education & professional experience

Date	**Event**
1994	Getting the higher education entrance qualification from the Heinrich-Mann Oberschule in Erfurt
1994 - 1996	Completion of the civilian service at the orthopedic hospital in Erfurt
1996 - 2000	Finishing the study of Biology at the University of Bayreuth Main subject: Animal Physiology Minor subjects: Genetic and Ecotoxicology
2000 - 2002	Diploma thesis with the title: "Die Bedeutung der Geschmacksrezeptoren der Termite *Schedorhinotermes lamanianus* bei der Wahrnehmung von Holzinhaltsstoffen" (Supervisors: Prof. Dr. von Holst and Dr. M. Kaib)
since 2003	PhD - student in the Lab of Cognitive Neuroscience (Prof. Dr. H. A. Mallot) at the University of Tübingen
2003 - 2006	Fellow of the Graduiertenkolleg 778 - "Kognitive Neurobiologie"
2007	Dr. rer. nat. in Biology: "Gaze control and cognitive load in active vision - Task specific strategies in normal and visually impaired subjects"
since 2008	Scientific Assistant in the Lab of Cognitive Neuroscience (Prof. Dr. H. A. Mallot) at the University of Tübingen

Academic distinctions

2003 - 2007	Stipend from the Graduiertenkollegs Kognitive Neurobiologie, Tübingen
2008	Poster award winner (IK2008 Conference)
2008	PhD award (Reinhold-und-Maria-Teufel Stiftung)
2009	Poster award winner (IK2009 Conference)

Teaching activities (since 2005)

Supervision of students at the Lab of Cognitive Neuroscience (University of Tübingen):

- 3 PhD theses (two still in progress)
- 14 Diploma theses
- 2 Master theses
- 11 Bachelor theses
- 3 Exam theses (accreditation work for teachers)
- 5 other theses (lab rotation, project study, student research project)

Teaching

- Practical Course: Visual Cognition (Bachelor & Master; winter term)
- Practical Course: Animal Physiology - physiology of the heart (Bachelor; summer term)
- Practical Course: Großpraktikum (Master Neurobiology; summer term)

- Seminar: Sprachliches- und nichtsprachliches Denken (summer term 2011)
- Seminar: Raum- und Zeitkognition (summer term 2012)
- Seminar: Raum- und Zeitkognition (summer term 2013)
- Seminar: Kognition bei Tieren und Menschen (summer term 2014)
- InstitutsSeminar: Seminar of the Department of Neurobiology (every summer & winter term)

- Mentoring Programme: for Bachelor students 1st and 2nd semester (winter term 2012)

10 Statements

nach §5(1) Ziff. 5-7 der Habilitationsordnung der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Tübingen in der Fassung vom 15. April 2013.

Ziff. 5-1: Ich versichere, dass ich die Habilitationsschrift, bzw. die von mir vorgelegten wissenschaftlichen Arbeiten, soweit sie von mir allein verfasst sind, selbständig und ohne andere als die darin angegebenen Hilfsmittel angefertigt habe. Ich versichere, dass bei den gemeinsam mit anderen Autoren verfassten wissenschaftlichen Arbeiten die gemäß Punkt 1 beschriebenen Anteile an den wissenschaftlichen Arbeiten selbständig und ohne andere als die darin angegebenen Hilfsmittel angefertigt wurden.

Ziff. 5-2: Ich versichere die Vollständigkeit des Verzeichnisses der wissenschaftlichen Veröffentlichungen.

Ziff. 6: Ich erkläre, dass ich bisher noch kein Habilitationsverfahren eingeleitet habe (und dass somit kein Habilitationsverfahren anhängig oder erfolglos beendet ist).

Ziff. 7: Ich erkläre, dass ich bisher nie strafrechtlich oder disziplinarrechtlich verurteilt wurde, und dass keine Straf- oder Disziplinarverfahren gegen mich anhängig sind (soweit die Auskunftspflicht nicht durch § 51 des Bundeszentralregister-gesetzes ausgeschlossen ist).

Tübingen, den 10. Dezember 2014

Dr. Gregor Hardiess