SPATIAL REMAPPING MECHANISMS

AND THEIR IMPAIRMENTS IN

PATIENTS WITH RIGHT PARIETAL LESIONS

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I. CHAPTER

SYNOPSIS

1. General introduction

Following a train with the eyes is apparently not the same as fixating a tree next to the tracks with the eyes while the train passes by. In the first case the retinal image of the train would stay (more or less) the same while in the second case it would move across the retina. However, in both cases we would have had experienced that the train had passed by and that it had moved through an otherwise (more or less) stationary landscape.

The perceptual experience of a stable world despite moving objects and despite self-movements is a prerequisite for acting in and interacting with the external world. The question how the visual system brings about stable spatial perception is hence often asked, and subject to theories and experiments from early days on.

Basically, information from three main sources were suggested to contribute to perceptual stability: Visual information in retinal images, command signals from the brain to the eye muscles (“efference copy signals”), and proprioceptive input. Each source of information by itself had been found to be insufficient to provide a stable perception of the environment. Retinal images of the environment are altered along with changes in the environment and self-movements. Thus, retinal information by itself would leave us with a disrupted spatial constancy, and moreover with the problem how to distinguish whether given retinal changes are due to changes in the outside world or due to self-movements. Classical attempts to answer how stable perception is achieved draw on concepts of “neural outflow” and “neural inflow”.

In the following, these concepts are explained and subsequently referred to in an outline of traditional theories about perceptual stability. Tied in with this more general introductory part, the theory of spatial remapping by Pisella and Mattingley (2004), seminal for the studies presented in the present thesis, and priming of pop-out utilised as an experimental paradigm to investigate spatial remapping abilities are introduced. The current chapter rounds off with an overview of studies 1 – 3, presented in the II. – IV. chapter.

1. 1 Concepts to explain the achievement of visual stability

Very early approaches (for a historical review see Grüsser, 1986) towards the formation of concepts that explain the interaction of the eye and objects in the outside world in order to construct stable spatial perception date back to Plato (428 – 348 B.C.). He assumed the site of this interaction to be localised in the extra-personal space. Early ideas were constantly elaborated until they vanished into oblivion when their foundation – the idea of an eye generated fire or "pneuma" - turned out to be not tenable in the early 18th century.

1. 1. 1 "Neural outflow hypothesis"

Conceptions that explain what information is used to construct visual stability have then emerged during the early 19th and 20th century.

When Aristotle's (384 – 322 B.C) ancient observation of an afterimage which moves with the eye was re-discovered (Darwin, 1786; Bell, 1823; Purkinje, 1825; von Helmholtz, 1867; Mach, 1906) the formation of the crucial concept of "efference copy signals" started to develop. Von Helmholtz´s interpretation of the moving after-image were further based on an earlier report by the ophthalmologist Albrecht v. Graefe (1828 – 1869) about a patient with palsy of his external eye muscle who stated to perceive motion of objects in the direction of an intended (however hindered) eye movement (v. Helmholtz, 1896), and on the phenomenon that when one tips one's eye-ball gently with the finger the external world destabilises (v. Helmholtz, 1867). He concluded that spatial calculations (e.g. object positions with regard to one's own position) emanates from what he termed "Willensanstrengung" (v. Helmholtz, 1867). The concept of "Willensanstrengung" matches the concepts of - nowadays commonly referred to as - "corollary discharge" (Sperry, 1950) and "efference copy" (v. Holst & Mittelstaedt, 1950), as explained in the following.

Basically, two conditions of movement perception are distinguishable, e.g. in the introductory scene picturing the by-passing train. Firstly, when we follow a moving object (e.g.

the by-passing train) with the eyes, “efference copy signals” or “corollary discharge” (i.e. copies of the motor commands that were given from the brain to the eye muscles) are added to the (more or less) stationary retinal signals. The result is commonly referred to as “efferent movement perception”. Secondly, the eyes are (more or less) motionless (e.g. when fixating the tree next to the tracks) and a moving object (e.g. the by-passing train) generates a retinal movement signal. This is termed “afferent movement perception”. During exploration we normally switch between both conditions. Stability of the visual world is perceived when the retinal change and the “neural outflow” correspond.

1. 1. 2 “Neural inflow hypothesis”

Kinaesthetic information which is received by mechanoreceptors of orbital structures, e.g. eye muscles, interacts with afferent movement or nerve fibre signals, i.e. inflow. This is another idea of how information about changes on the retina might be provided. It was proposed by Sherrington (1918) who suggested *“that the proprioceptive nerves of the eyeball muscles […] contribute to space as perceived with the eye”* (p. 332). Evidence for his assumption was drawn from conclusions by analogy to other, e.g. the tactile, modalities. *“Let three points, say the prong-tips of a trifid fork, be set against the skin [...]. One can perceive tactually not only that the points are three, and that they lie equidistant in one straight line, but, with approximate correctness, the orientation of that line to the vertical—also, of course, the whereabouts in the field of reach of the hand at which the touch is met. In this case the contribution made to the spatial perception by the muscular sense is well known and no longer debated.*” (p. 336).

Experimental evidence (e.g. Lackner & Shenker, 1985; for reviews see e.g. Matthews, 1982; Weir, 2000; 2006) for the achievement of visual stability by “inflow signals” as well as constraints (e.g. in complex scenes Pelz & Hayhoe, 1995) had been shown. However, theories of visual stability outlined below are rather based on the “neural outflow” than on the “inflow hypothesis”.

1. 2 Classical approaches

Solutions concerning the problem of perceptual stability despite eye-movements by which the retinal images are shifted from pre- to post-saccadic positions were basically framed by four theoretical main ideas about how information (e. g. retinal image, efference copy signal) is used in order to maintain or achieve perceptual stability.

1. 2. 1 The idea of elimination

The basic assumption with this idea is that effects concomitant with eye movements must be eliminated. That had been suggested to be accomplished by the interplay of “efferent” and “afferent signals”. V. Holst and Mittelstaedt (1950) devised the “reafference principle”. The “eye movement command” sent to the eye muscle entails an “efference copy”. Information about the retinal shift caused by the eye movement in turn provides a “reafference”. In mathematical terms the “efference copy signal” is supposed to have a positive (´+´), the “reafference” a negative (´-´) algebraic sign. Subtraction of both should result in zero, thus cancel out the effects caused by an eye movement in perception, with the outcome of perceptual stability.

1. 2. 2 The idea of translation

The basic assumption here is the existence of a memory which contains a representation of the world in terms of spatiotopic coordinates (“memory fusion hypothesis”). “Neural outflow” presets the algorithm for the translation of current (transient) information provided by retinal representations into more enduring higher-order spatiotopic (or world) coordinates (e.g. Bischof & Kramer, 1969).

The idea would provide an explanation why the world is perceived as stable, however, although it is widely accepted that memory plays a role in visual perception (e.g. Maljkovic & Nakayama, 2000), the idea of a higher-order spatiotopically organised memory was not supported (Irwin, Zacks, & Brown, 1990; Rensink, 2000).

1. 2. 3 The idea of evaluation

In the framework of this approach the recognition of change is vital. MacKay (1973) proposed a "*mechanism for updating the internal representation (whatever that may be)*" (p. 523) to operate according to the principle of rejecting a statistical "null hypothesis" which assumes stability. "Efference copy signals" are needed in order to evaluate when the "null hypothesis" has to be rejected to support the alternative hypothesis of instability, and hence indicate the necessity to update the internal representation.

1. 2. 4 The idea of calibration

Bridgeman, van der Heijden, and Velichkovsky (1994) argue that the problem of how perceptual stability across saccades is achieved can be reduced to the problem of how perceived positions from successive eye fixations calibrate retinotopic maps across eye movements. The calibration is assumed to be accomplished by different mechanisms which use information from different sources according to the perceptual conditions and the behavioural (e.g. motor) requirements.

Rather than assuming the necessity of corrections of the whole perception of the outside world along with eye-movements the model assumes selective calibration of features (e.g. only the position of an object but not its colour or shape) represented on retinotopic maps from one fixation to the other.

The model includes the consideration that early information from retinotopic maps which code elementary features (such as position, orientation, colour etc. of an object) are mapped into a more common non-topographic representation as proposed by Koch and Ullman (1985).

2. A theoretical framework of spatial remapping mechanisms

More recent models agree with the idea that visual input provided with each eye fixation is integrated across space and time by updating representations of the external world on a more central map. The mechanisms involved in updating processes became subject of interest (Colby, Duhamel, & Goldberg, 1995, Rensink, 2000; Pisella and Mattingley, 2004; Gottlieb, 2007).

Insights about mechanisms operating in healthy organisms are often provided by patients who demonstrate dissociable impairments among preserved abilities. The various symptoms assigned to the neglect syndrome, a neurological disease often following lesions to the right parietal lobe with the core component of an inability to detect or to respond to stimuli in the contralesional hemi-field (Kerkhoff, 2001; Karnath, Milner & Vallar, 2002; Mort, Malhotra, Mannan, Rorden, Pambakian et al., 2003) for instance had crucially influenced research of spatial processing (see e.g. Husain & Rorden, 2003).

Recently, Pisella and Mattingley (2004) suggested that a component that might underlie some phenomena associated with neglect were spatial remapping impairments. This assumption provided the initial point for developing a theoretical conception of spatial remapping mechanisms which operate on a saliency map (Itti & Koch, 2001) embedded between two stages of visual processing (Niebur & Koch, 1998).

2. 1 Saliency map

Given processing capacity limitations of the brain visual input needs to be selected according to its eventual behavioural relevance, so that relevant information is further available for higher visual processing. Moreover, the order of processing of the selected information has to be determined. Selection and ordering is accomplished by mechanisms of selective attention. These are driven by the saliency of the stimuli in a visual scene. Stimuli in a given location are rendered salient in a bottom-up manner (albeit top-down modifiable, see Müller, Reimann, & Krummenacher, 2003), i.e. from immediate sensory input, according to the difference of their

visual features (e.g. colour, orientation, motion) from the visual features of stimuli in other locations (Parkhurst, Law, & Niebur, 2002, Constantinidis, Christos, & Steinmetz, 2005). The information derived from the different features of stimuli have been proposed to be depicted onto feature maps, and subsequently combined and integrated into a saliency map which provides a global measure of conspicuity of a visual scene along which selective attention is deployed (Itti & Koch, 2001; for a similar concept see e.g. the "master map" postulated by Treisman & Gelade, 1980 in the framework of the "Feature Integration Theory"). A thoroughgoing example of a salient stimulus is the target in a pop-out visual search display (see below, p. 20). After the most salient stimulus has been selected, activity on the saliency map at the selected location is suppressed and the location of the next-highest salient stimulus on the saliency map is attended to and so on (Itti, 2000).

2. 2 Two stages of visual processing

According to a model proposed by Niebur and Koch (1998) visual processing comprises two stages. Processing elementary visual features like colour, motion, contrast etc., extraction of these features across all locations in the visual scene onto feature maps, and their encoding on a common saliency map in a parallel manner takes place in the early first stage. In the later second stage attention is allocated (overtly and covertly) to different spatial locations of the saliency map in a serial manner. The second stage works according to a winner-takes-all principle with only the most salient elements above a threshold entering conscious space representation ("spatial array").

2. 3 Spatial remapping

Between the first and the second stage of visual processing, spatial remapping mechanisms were suggested to operate in order to allow for spatio-temporal contingency between successive visual images, encompassing also two processes. During the first process,

information of the current representation on the saliency map which has to be integrated into the following representation is selected. Selection takes place on the basis of a probabilistic threshold applied to the amount of activity on the saliency map above which an item is protected from being overwritten on the saliency map. During the second process the selected information is re-positioned or re-freshed on the map along with overt and covert shifts of attention, respectively.

2. 4 The neuroanatomy of spatial remapping

Neurophysiological findings of the selective responsiveness of monkeys´ neurons in the lateral intraparietal area (LIP), that show that these neurons respond only to either salient, e.g. by sudden onset or behaviourally relevant stimuli, suggest a selective, rather sparse, representation of space (Gottlieb, Kusunoki, & Goldberg, 1998). This matches nicely with the theoretical conception of visual scene representation on a saliency map in the first stage of visual processing as suggested by Niebur and Koch (1998). Hence, Pisella and Mattingley (2004) suggest the parietal cortex as the neural correlate of the saliency map upon which spatial remapping mechanisms operate. More particularly, they suggest the superior parietal lobe (SPL) as the neural correlate for the saliency map based on the observation that application of transcranial magnetic stimulation to the left and right SPL lead to extinction[1]-like phenomena in healthy subjects in the contralateral hemi-field of stimulation (Pascual-Leone, Tortosa, Grafman, Always, Nichelli et al., 1994).

The area of the inferior parietal lobe (IPL) was proposed to provide the neural correlate for the conscious representation of the spatial array (second stage of visual processing according to Niebur & Koch, 1998) e.g. based on findings that the IPL is involved in change blindness (see below; Beck, Rees, Frith, & Lavie, 2001).

[1] Extinction describes the phenomenon – often observed in patients recovered from acute neglect after right-hemispheric lesions - that when stimuli are presented bilateral simultaneously, contralesional stimuli are going unnoticed, while on the contrary stimuli in both hemi-fields are perceived when they are presented unilaterally (Kerkhoff, 2004).

2. 5 Spatial remapping deficits after parietal lesions

According to a contralateral spatial representation in the parietal cortex (Sereno, Pitzalis, & Martinez, 2001) remapping deficits occur after both, left and right parietal lesions. Based on the notion that the right hemisphere can direct attention in both left and right visual fields, whereas the left hemisphere can direct attention only in the right visual field (Heilman & Van Abdell, 1980) right parietal lesions were proposed to have a more dramatic effect compared to left parietal lesions.

Accordingly, Pisella and Mattingley (2004) assume in their model that following left parietal lesions left and rightward directed saccades lead to overwriting of information on the contralateral side of the saliency map, respectively. Following right parietal lesions rightward saccades lead to an overwriting of information on the contralateral side while leftward saccades lead to an overwriting of the whole saliency map (see Pisella & Mattingley, figure 8, p. 192). The overwritten information on the saliency map is hence not available for the next processing stage, and consequently not available for conscious representation.

Evidence is drawn from results of parietal patients in double step saccade tasks (Duhamel, Goldberg, Fitzgibbon, Sirigu, & Grafman, 1992a; Heide, Blankenburg, Zimmermann, & Kömpf, 1995). The task requires the performance of two subsequent saccades to two targets. Targets are only briefly flashed and not visible throughout the performance of the task. The first saccade has to be conducted from the fixation point to the first target and can be encoded in retinal coordinates. The second saccade to the second target has to be conducted from the location of the first, and hence, it must be calculated from a new viewing position. For the calculation of the second saccade, information can not be encoded in retinal coordinates, but requires remapping of the visual scene. Patients with parietal lesions were shown to perform intact first but deficient second saccades. However, patients with left parietal lesions showed intact first and second saccades when fixation cross and saccadic targets were within the same

hemi-field whereas patients with right parietal lesions conducted a deficient second saccade in the condition where both targets were presented within the left hemi-field (Heide et al., 1995).

2. 6 Contribution of spatial remapping deficits to visual search impairments in neglect

Pisella and Mattingley (2004) point out to a number of phenomena occurring within the wide scope of neglect symptoms which are not satisfyingly explainable offhand by attentional and representational neglect theories. Among them the phenomenon of “ipsilesional” neglect after left orienting (Mattingley, Pierson, Bradshaw, Phillips, & Bradshaw, 1993), i.e. when neglect patients bisect lines atypically to the left of the centre after being cued towards the left end of the line, or fail to report right-sided stimuli. Furthermore, “productive” manifestations, i.e. perserverative behaviour in the “intact” hemi-space, e.g. repeated cancellation of lines on the right side in a line cancellation task (Rusconi, Maravita, Bottini, & Vallar, 2002), the striking behaviour of revisiting already searched locations during visual search (Husain, Mannan, Hodgson, Wojcuilik, Driver et al., 2001), or spatially disorganised search strategies with numerous repetitions of search paths (Wojciulik, Husain, Clarke, & Driver, 2001). Furthermore, size distortion (Milner & Harvey, 1995) and space compression (Halligan & Marshall, 1991),

Deficient spatial remapping mechanisms, in accordance to the model proposed by Pisella and Mattingley (2004) might account for the above mentioned phenomena in neglect. According to the model, an impaired first spatial remapping process would cause truncated visual representation of a scene, and consequently, stimuli would be prevented from reaching the level of conscious representation. In the event of an impairment of the second process the updating of selected visual information along with changes in retinotopical coordinates would fail, and behaviourally result in neglect performance.

The model clearly explains clinical observations of neglect patients´ behaviour in visual exploration. Moreover, deficient spatial remapping provides a plausible explanation for the lack of awareness for left-sided stimuli in those patients.

2. 7 Spatial remapping abilities and their limitations in healthy persons

Pisella and Mattingley (2004) suggested that change blindness, a failure to notice changes in a visual scene under certain circumstances in healthy subjects basically reflects the nature of spatial remapping.

Change blindness in healthy subjects and hemi-spatial neglect in patients with (most frequently) parietal lobe lesions have in common that visual information is received by primary visual areas whereas a subset of visual information is not detected consciously (Pisella & Mattingley, 2004).

In the case of change blindness, elements which occur at a location in a visual scene which is not attended to are not represented on the saliency map in the first stage of visual processing, and are not available for conscious representation in the second stage of visual processing. Thus they are not available for conscious report. Anatomically consistent with this notion, the parietal, particularly the right parietal cortex has been shown to be crucially involved in conscious change detection (Beck et al., 2001; Beck, Muggleton, Walsh, & Lavie, 2006).

2. 8 The role of overt and covert attention

The model by Pisella and Mattingley (2004) assumes spatial remapping to be required after saccades, which are by nature accompanied by overt shifts of attention and after covert shifts of attention. The latter assumption is based on evidence from the phenomenon of change blindness which also occurs along with covert attention shifts, i.e. without accompanying eye movements, and not only after overt attention shifts. Further support for this assumption is drawn from the close linkage (e.g. indicated by common neural networks; Corbetta, Akbudak, Conturo, Snyder, Ollinger, et al., 1998) between overt and covert attention.

In their model, Pisella and Mattingley (2004) assume that spatial remapping mechanisms re-locate activations on the saliency map after overt shifts of attention and re-fresh them after covert shifts of attention.

3. Priming of pop-out as a method to investigate spatial remapping abilities

In order to investigate spatial remapping mechanisms and to test some of the model's assumptions we chose a priming of pop-out paradigm (Maljkovic & Nakayama 1994, 1996, 2000). The paradigm allows measuring the effect of experience from previous trials in current trials. Priming effects indicate integration of visual information across trials. In contrast, the absence of priming effects would indicate a failure in the integration process. In the presence of spatial remapping requirements between subsequent trials, a failure in the integration process would be attributable to deficient spatial remapping mechanisms.

In general, the task requires subjects to find a pop-out target among distractors in subsequently presented visual search displays. A pop-out target differs in a single feature attribute (e.g. colour; red in our experiments) from a set of homogeneous distractors (green in our experiments), among which it occurs, and therefore it "pops out" of the search display. The pop-out effect is based on the extreme salience of the target due to its unique difference compared to the surrounding distractors and hence the extreme fast bottom-up driven allocation of selective attention to the (pop-out) target. The effect results in a very fast response to the target, irrespective of the number of distractors (Treisman & Gelade, 1980).

It has been shown that RTs to pop-out targets are modifiable e.g. by location priming (Maljkovic & Nakayama, 1996). Targets appearing at previous target locations are detected faster and more accurately (facilitation), while detection of targets at previous distractor locations is slower and more error-prone (inhibition). We measured facilitation and inhibition relative to a baseline resulting from RTs to targets appearing at neutral (empty) positions.

The presence of these cross-trial priming effects indicates successful spatio-temporal integration of subsequent visual images (Chun & Nakayama, 2000). In conditions with intervening events requiring re-location or re-freshing of information on the saliency map between these trials, the presence of priming can thus be taken as evidence for successful integration based on successful spatial remapping.

Basically, the experiments in our studies were as follows: In subsequently presented visual search displays a red diamond shaped pop-out target was presented among green diamond-shaped distractor stimuli. The task was to indicate as fast and accurately as possible whether the red diamond-shaped target was cut off on the top or on the bottom by pressing an upper or lower button in accordance with the cut-off direction. Hence, the detection-driving feature was identical with the response-driving feature.

4. Introduction to the current studies

We analysed location priming effects, and thus the ability to integrate visual information across subsequent trials in the three studies presented in the following chapters.

Based on previous findings in healthy subjects priming effects occur under conditions that require no attentional shifts in-between subsequent trials, i.e. with the subject's fixation maintained and the search displays presented at retinotopically equal locations with respect to the fixation cross (Maljkovic & Nakayama, 1996; Geyer, Krummenacher, & Müller, 2007). In study 1 we tested whether location-based priming effects would outlive spatial shifts of attention in healthy subjects. The basic assumption, derived from Pisella and Mattingley´s (2004) account was they would, and that the outliving would be based on intact spatial remapping mechanisms operating in healthy subjects along with attention shifts. The aim of study 1 in view of further investigations in patients, i.e. in studies 2 and 3 was to test the suitability of the priming

paradigm to serve our purpose to investigate spatial remapping abilities, and furthermore, in patients, purported deficits.

To test whether priming effects would outlive saccadic shifts of overt attention, subjects had to re-fixate the fixation cross in turns on the left and on the right side of the monitor between subsequent trials. In two separate experiments priming effects were measured at post-saccadically retinotopic and spatiotopic locations, respectively, and compared to effects in a control experiment requiring no attention shifts. The experiments were also applied in study 2. To test whether priming effects would outlive covert shifts of attention subjects´ attention was distracted between subsequent trials while their fixation was maintained. In two separate experiments priming effects were measured after exogenous and endogenous distraction, respectively, and compared to a control experiment without distraction. The experiments were also applied in study 3. The presence of priming effects despite interfering attention shifts could be taken as evidence that processes that integrate visual information along with attention shifts, i.e. spatial remapping mechanisms, operate flawlessly in healthy subjects.

The aim of study 2 was to test whether the parietal cortex provides the neural correlate of spatial remapping as assumed by Pisella and Mattingley (2004). To that end, we tested whether spatial remapping deficits would occur after saccadic shifts of overt attention in patients with right parietal lesions. Deficits were expected to be indicated by altered or disturbed priming effects in those patients as compared to priming effects in healthy control subjects and furthermore, in patients with right-hemispheric lesions not involving the parietal lobe. Latter patients (without parietal lesions) were tested, to control for and differentiate between deficits occurring more generally after right-hemispheric damages and specific deficits occurring after right parietal damages. Moreover, given the crucial role of priming for visual search (Chun & Nakayama, 2000) disturbed priming as an indicator of deficient spatial remapping would provide support for the assumption made by Pisella and Mattingley (2004) that spatial remapping deficits

contribute to visual search impairments as they are often observed in patients with right parietal lesions.

The aim of study 3 was to test the model's assumption that spatial remapping is required after spatial shifts of covert attention. Again, we compared priming effects of patients with right parietal lesions to those of patients with right-hemispheric lesions without parietal involvement, and healthy subjects. We expected priming effects to be disturbed in patients with right parietal lesions provided that covert attention shifts induce spatial remapping requirements, and that the anatomical site of spatial remapping mechanisms operating to integrate visual information across spatial shifts of covert attention is located in the parietal lobe.

II. CHAPTER

STUDY 1

LOCATION PRIMING OUTLIVES OVERT AND COVERT SHIFTS OF ATTENTION

1. ABSTRACT

To increase effectiveness of visual information processing from the very first processing level, helpful mechanisms, reflected for instance by location priming effects, accompany visual search behaviour. In six experiments, we test the assumption that location priming effects as they occur in priming of pop-out visual search outlive saccadic shifts of overt attention and covert attention shifts. Location priming effects which were robustly present in a control experiment (1) were remapped along with saccades in-between sequential trials in both, retinotopic and spatiotopic coordinates (experiment 2 and 3). They were still present in a control experiment with prolonged interstimulus interval (ISI; experiment 4) and after exogenous shifts of covert attention induced by task-irrelevant peripherally presented distractors in-between trials (experiment 5). Furthermore, effects outlived covert shifts of attention even when an endogenous component, implemented by a secondary task conjoint with the peripheral distractors, was required (experiment 6).

The robustness of priming effects suggests their crucial role in exploring a dynamic environment, in terms of firstly, supporting post-saccadic visual processing in multiple reference frames and secondly, keeping track of encoding behaviourally relevant visual information despite distraction of attention.

2. INTRODUCTION

Searching for relevant information in a dynamic environment requires highly flexible adaptation to constant changes. At least two basic problems are encountered. Firstly, it requires constant updating of visuo-spatial information along with changes in the environment and self-movements, such as saccades. The question that arises is how stable visual representations are achieved despite overt shifts of attention, by definition accompanied by saccades. Visual stability, in turn, can be considered as a prerequisite for rediscovering stimuli which have changed locations or redirect gaze to objects at invariant locations. Secondly, the representation of relevant information needs to be protected from interference by distracting stimuli and non-relevant information. This refers to the problem of keeping track one's eyes with relevant information despite spatial shifts of covert attention, with the latter being important for discovering eventual relevant information.

Neurophysiological studies in monkey provide evidence for neurons in the lateral intraparietal area (LIP) and frontal eye fields (FEF) which compensate for overt attention shifts by exhibiting predictive remapping. That is, they discharge before upcoming saccades bring visual target stimuli into their receptive fields (Duhamel, Colby, & Goldberg, 1992b). Thereby, enlargement of the neurons´ effective receptive fields occurs into the specific directions of the intended saccades (Kusunoki & Goldberg, 2003), just as if the effective receptive fields move ahead of the saccades, predicting the post-saccadic retinal coordinates of target stimuli (Melcher, 2007). Furthermore, memory-based remapping takes place in area LIP (Duhamel, et al., 1992b; Heiser & Colby, 2006) and in extra-striate areas (Merriam, Genovese, & Colby, 2007). That is, neurons discharge to the short-term memory trace of stimuli, when saccades bring locations into their receptive fields, which were previously occupied by the stimuli. Hence, stimulus representations are remapped by predictive and by memory-based remapping. But do these remapping processes influence visual perception, and if so, how? The question arising with regard to overt attention shifts is where after saccades (i.e. in terms of spatial

coordinates post-saccadically) processing of visual information is influenced. Effects of masking iconic memory contents had been found to be transferred into retinotopical and spatiotopical coordinate systems (McRae, Butler, & Popiel, 1987). There is also evidence that information about visual features such as motion (Melcher & Morrone, 2003) and form (Melcher, 2005), is transferred across saccades. It has been suggested that information transfer is accomplished by remapping (Gottlieb, 2007), with form integration modulated by stimulus complexity (Melcher, 2005). Consistently remapped information can be tracked down in visual cortical areas such as V3A, hV4, and also to a small extent in V1 and V2 (Merriam et al., 2007).

Interestingly, inhibition of return, an inhibitory tag, considered to mark already explored stimuli in order to enhance visual search performance by supporting advancement of visual search towards not yet explored stimuli; and as such similar in function to inhibition in a priming of pop-out paradigm (Maljkovic & Nakayama, 1996; Klein & MacInnes, 1999) has been found to be remapped in retinotopical and environmental coordinates after saccades (Sapir, Hayes, Henik, Danziger, & Rafal, 2004). The result found by Sapir et al. (2004) provides evidence that supportive implicit memory mechanisms in visual search (Maljkovic & Nakayama, 2000; Shore & Klein, 2001) might be preserved after shifts of attention.

In the present study we investigate the effects of overt and covert shifts of attention on location-based effects in a visual priming of pop-out paradigm (Maljkovic and Nakayama, 1996). Location priming accompanies visual search. Allocation of spatial attention is modulated differentially according to previously made experience. Hence, facilitatory and inhibitory effects are measurable in a given trial as a function of the preceding trial: Targets are detected faster and/or more accurate at previous target locations (facilitation), while they are detected slower and/or more error-prone at previous distractor locations (inhibition), compared to targets at previous empty locations (baseline). Most commonly, tasks are administered in

conditions without varying eye movements or attentional distraction (e.g. Geyer et al., 2007). It is not clear how these effects are affected by overt and covert attention shifts.

Evidence suggests overlap of overt and covert attention in terms of neural correlates (Nobre, Gitelman, Dias, & Mesulam, 2000; Beauchamp, Petit, Ellmore, & Ingeholm, 2001) and function (Deubel & Schneider, 1996). However, despite this linkage, covert attention shifts were shown to have different impacts on neurophysiological mechanisms and visual perception compared to overt attention shifts. Receptive fields of parietal neurons in monkeys which remapped new retinal locations did not discharge in response to covert attention shifts to the new locations but only when actual saccades were conducted (Duhamel et al., 1992b). Spatio-temporal transition of invariant object recognition (Cox, Meier, Oertelt, & DiCarlo, 2005) and form adaption (Melcher, 2007) was differently affected by covert and overt attention shifts. The exact boundaries of the interplay of overt and covert attention are not yet clarified (e.g. Perry & Zeki, 2000; Nobre et al., 2000).

We were interested whether location priming effects outlive goal-directed saccades and/or attention distraction between the trials, and whether they are affected differentially by overt and covert attention shifts, respectively. Furthermore, we were interested whether facilitation and inhibition might be affected differentially by attentional shifts. As it has been shown the two effects are likely to reflect two dissociable mechanisms, given their differential susceptibility to different factors. In particular, set size (Geyer & Müller, submitted) and irregularity of stimulus arrangements (Geyer et al., 2007) were found to affect inhibition but not facilitation. In order to make both, facilitation and inhibition investigatable in the present experiments, we used search arrays with equally spaced stimuli.

We analysed facilitation and inhibition in six experiments. Firstly, the “control experiment” (1) with a centrally presented visual search array around a central fixation cross, involving no shifts of attention. Secondly, the “retinotopic experiment” (2) with a visual search array around a fixation cross switching in turns to the left and the right side of the monitor, thus requiring a

saccade between the trials in order to re-fixate the fixation cross but nevertheless preserve the retinotopy of visual search arrays. Thirdly, the “spatiotopic experiment” (3) with a centrally presented visual search array to be viewed from a peripheral fixation cross presented in turns on the left and on the right side of the monitor (and the search array), requiring a saccade between the trials in order to re-fixate the fixation cross, and additionally the viewing of the search array from a location different in retinal but equal in spatial coordinates. Fourthly, the “long ISI control experiment” (4), equivalent to the “control experiment” but with a longer ISI, adapted for the needs of experiment 5 and 6, in which visual distractor stimuli were presented in-between the trials and hence more time was needed between subsequently presented trials. Taken into account that there is evidence that covert attention shifts occur by support of two distinct mechanisms, reflexive orienting towards exogenous and voluntary orienting towards endogenous stimuli (Müller & Rabbitt, 1989) attention was distracted exogenously and endogenously in experiment 5 and 6, respectively. Thus, fifthly, the “irrelevant distractor experiment” (5) presented task-irrelevant (exogenous) distractors randomly in the left or right periphery in-between the trials. Sixthly, the “relevant distractor experiment” (6) was equivalent to experiment 5 but with a secondary task (hence with an adherent endogenous component) conjoint with the peripheral distractors.

3. CONTROL EXPERIMENT (1)

3. 1 Method

3. 1. 1 Participants

10 observers (5 male, mean age 31.8; *SD* = 13.81) with normal or corrected-to-normal visual acuity participated in the experiment. All subjects gave informed consent to participate in the study.

3. 1. 2 Materials

A search display (see figure 1) consisted of three stimuli, one red target and two green distractors. The stimuli, presented on a black background (0.5 cd/m^2 in luminance), were near-equiluminant (red: 7.7 cd/m^2; green: 8.0 cd/m^2) and diamond-shaped (size: 1.2° of visual angle). All stimuli had a (response-relevant) cut-off section (size: 0.3°) at either the top or the bottom. The cut-off sections were determined randomly and independently for each target and distractor stimulus. The search elements were arranged on a near-circular 'ellipse', with horizontal and vertical axes of 17.5° and, respectively, 14.0°, around a white fixation cross (size: 0.5° x 0.5°; luminance: 13.7cd/m^2). The target could appear at one of a total of six possible locations on the circumference of the ellipse. The distractors were then positioned such that the distances between adjacent stimuli on the circumference (target-distractor and distractor-distractor distances) were equal, i.e., the separation between adjacent locations was 6/3 = 2, with one intervening location. With respect to the previous trial *n-1*, targets on trial *n* appeared at one of three types of position: at the same position as the target on the previous trial, at the position of a distractor on the previous trial, or at a position that was empty on the previous trial (neutral baseline). Stimulus presentation and response registration were controlled by a standard computer. Subjects responded with a standard two-button mouse connected to the computer via the serial port. The mouse was fixed on the table in front of the

subject, rotated by 90° such that the ‘left’ mouse button could be used as the ‘upper’ (top section cut off) and the ‘right’ button as the ‘lower’ (bottom section cut off) response key. Observers viewed the monitor from a distance of approximately 55 cm, with head position maintained by the use of a head and chin rest.

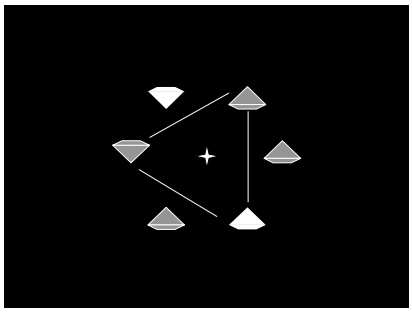


Figure 1. *Illustration of the search displays used in the present experiment. The red target (depicted as white diamond) appeared together with two green distractors (depicted as gray diamonds) in either the left or right visual field. One possible search display is indicated by the connecting lines between the stimuli, another display is shown without connecting lines.*

3. 1. 3 Procedure

At the beginning of each trial, a blank screen with just the fixation cross in the centre of the monitor was presented. The fixation cross remained on all the time. After 1,000 ms, the search display was presented and remained visible until the subject responded (see figure 2). The task was to press the upper/lower response key as fast and as accurately as possible according to the position (top/bottom) of the cut-off target section. Each display remained visible until subjects responded. RTs and errors were recorded. Error feedback was not provided. Subjects were instructed verbally and tested individually. The experiment consisted of 384 experimental trials, presented in 4 blocks of 96 trials each, with a minimum 10-s break after each block. The experimental session was preceded by a practice block of 96 trials (data not recorded). The whole experiment lasted about 30 minutes.

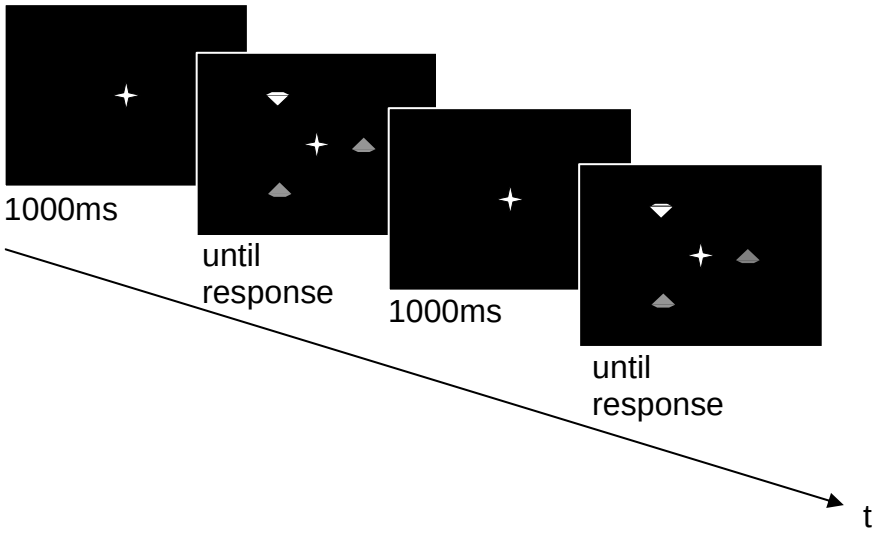


Figure 1. *A fixation cross was presented, followed by the visual search array around the fixation cross, displaying the red target (depicted as white diamond) and the two green distractor stimuli (depicted as gray diamonds).*

3. 2. Results and discussion

The dependent variables RTs (excluding error trials and trials following an error trial as well as extreme values of 2 standard deviations above or beneath mean RTs of the respective target position) and accuracy (error percentage rate; err%) were examined in separate ANOVAs with the within-subject factors Target Position (target at previous target location, at previous distractor location, at previously empty location) and Side (target in left, in right hemi-field). Level of significance was 5%.

Reaction times

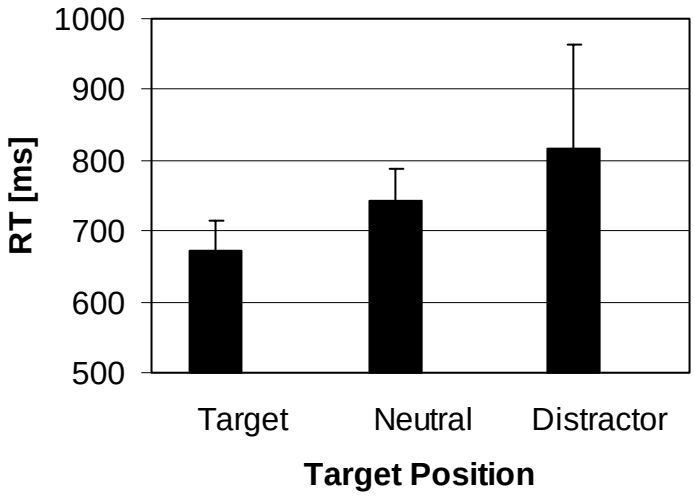


Figure 3. *Mean reaction times (RT) at the three target positions (target, neutral, and distractor). Error bars indicate standard errors.*

The ANOVA of RTs revealed the main effect of Target Position to be highly significant [$F(2, 8) = 71.68$, $p < .01$]. RTs at previous target positions (M = 672.12 ms, SD = 132.92) were highly significantly lower ($t(9) = -7.07$; $p < .01$), while RTs at previous distractor positions (M = 816.15 ms, SD = 146.38) were highly significantly higher ($t(9) = -8.08$; $p < .01$) compared to RTs at neutral positions (M = 742.68 ms, SD = 146.38), indicating both facilitation and inhibition.

Accuracy

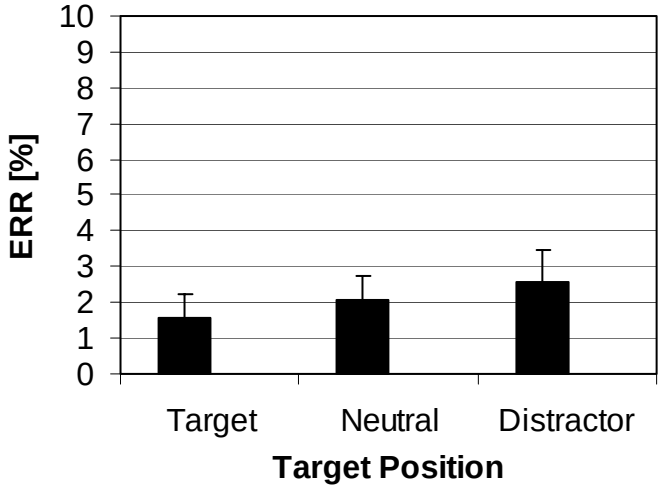


Figure 4. *Error percentage rates (err%) at the three target positions (target, neutral, distractor). Error bars indicate standard errors.*

The ANOVA for accuracy (as depicted in figure 4) revealed no significant main effect of Target Position ($p > .35$). The task was considerably easy, which accounts for the low error rate.

The RTs results are congruent with results of previous studies of location priming (e. g. Maljkovic & Nakayama, 1996; Geyer et al., 2007). They show that under static conditions attention is allocated faster to locations which were previously occupied by target stimuli in contrast to slowed allocating of attention towards locations which were previously occupied by distractor stimuli. In order to compare magnitude of facilitation and inhibition, we calculated priming effects relative to the overall RTs (in percent). Relative facilitation (M = -9.56 %; SD =

3.99) was nearly equal the size of relative inhibition (*M* = 10.08, *SD* = 3.79), indicating that inhibition was similar in extent to facilitation in the control experiment.

In experiment 2 and 3 we tested whether overt shifts of attention towards a different spatial location would alter location priming. We were interested in both, whether effects outlive attention shifts at all, and if so, whether facilitation and inhibition would be affected differentially. The “retinotopic experiment” (2) was designed to measure priming effects at retinotopically equal locations after overt attention shifts.

4. RETINOTOPIC EXPERIMENT (2)

4. 1 Method

4. 1. 1 Participants

10 observers (5 male, mean age 32.40; *SD* = 14.33) with normal or corrected-to-normal visual acuity participated in the experiment. All subjects gave informed consent to participate in the study.

4. 1. 2 Materials

Stimuli were basically the same as in the "control experiment" (1) with the difference that they appeared either in the left half or in the right half of the monitor screen (8.2° of visual angle peripherally; see figure 5). To compensate for the fact that two visual search displays were presented in turns on the left and on the right side of the screen, but virtually had to match monitor size, search displays were designed adaptively 20% smaller than the size of the originally search display of the "control experiment" (1). In order to keep the size of the stimuli perceptually comparable to experiment 1, subjects viewed the monitor from 20% less distance (44 cm) compared to the distance of experiment 1.

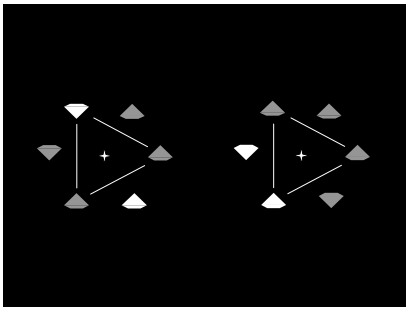


Figure 5. *Six stimuli positions around a fixation cross in the left or the right half of the monitor screen, respectively, were possible. The three stimuli (one target, two distractors) appeared either around the fixation cross in the left half or the right half of the screen, with the presentation side switching from trial to trial.*

4. 1. 3 Procedure

The procedure was basically the same as in the “control experiment” (1) with the exception that a saccade to the fixation cross on the opposite side (in turns from left to right and from right to left) of the screen was required between the trials (figure 6). Subjects were instructed to saccade in turns from left to right and from right to left, accordingly. During the experimental trials, correct re-fixations were controlled online by the experimenter using a mirror.

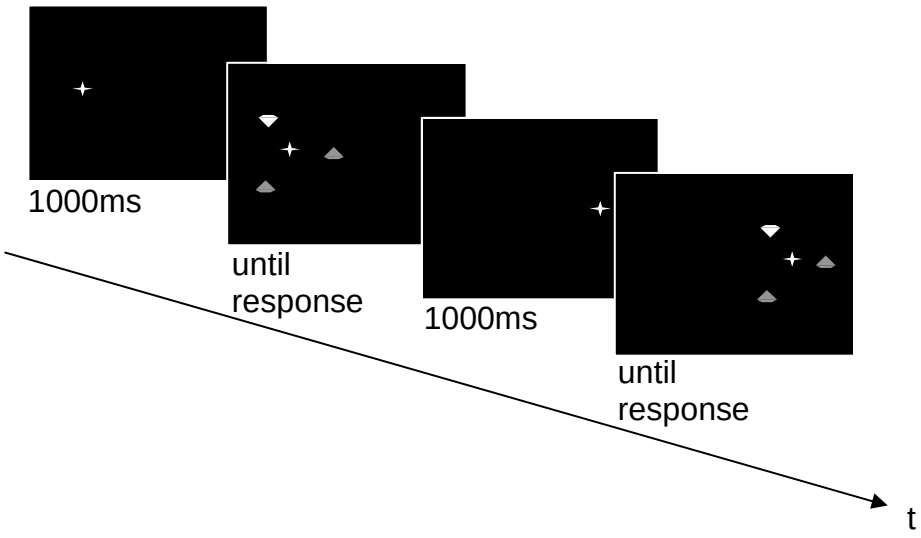


Figure 6. *A fixation cross was presented in turns on the left or on the right side, followed by the visual search array around the fixation cross, displaying the red target (depicted as white diamond) and two green distractor stimuli (depicted as gray diamonds).*

4. 2 Results and discussion

The same analyses were calculated as in the “control experiment” (1).

Reaction times

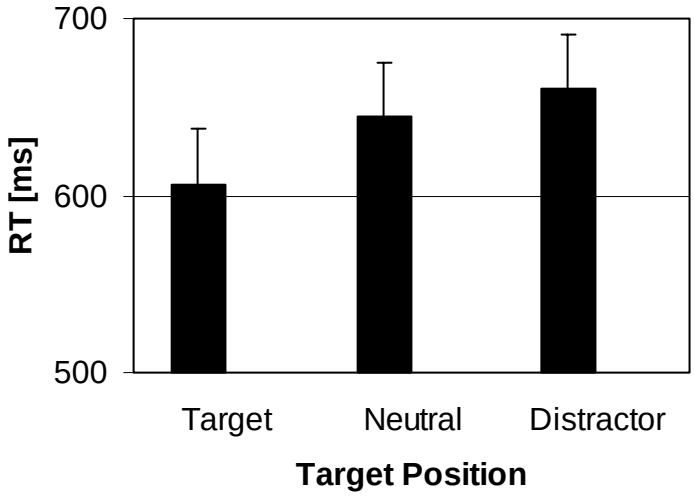


Figure 7. *Mean Reaction times (RT) at the three target positions (target, neutral, and distractor). Error bars indicate standard errors.*

The ANOVA for RTs (as depicted in figure 7) revealed the main effect of Target Position to be highly significant. [$F(2, 8) = 22.44$, $p < .01$]. RTs at previous target positions were highly significantly lower ($t(9) = -4.69$; $p < .01$), while RTs at previous distractor positions were significantly higher ($t(9) = -2.41$; $p < .05$) compared to RTs at neutral positions, indicating facilitation and inhibition.

Accuracy

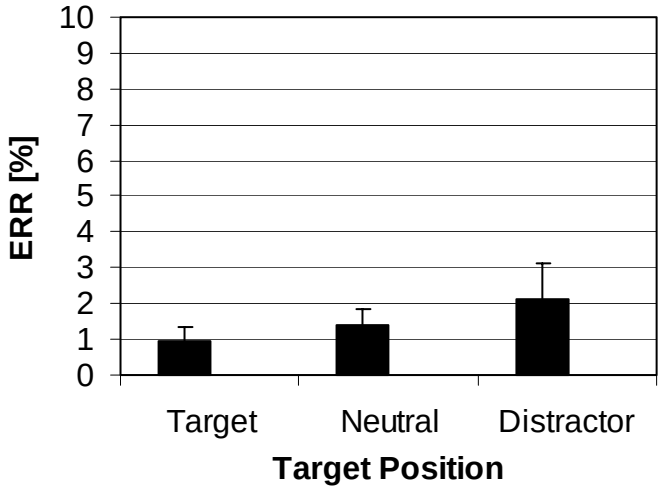


Figure 8. *Error percentage rates (err%) at the three target positions (target, neutral, distractor). Error bars indicate standard errors.*

Accuracy (as depicted in figure 8) was low (M = 1.48%; SD = 1.75) and comparable (p > .45) to accuracy of the "control experiment" (M = 2.07%; SD = 2.05). ANOVA revealed no significant main effect of Target Position (p > .25).

RT pattern revealed priming effects to be transferred into retinotopically equal locations after saccades. The result is in line with previous results suggesting the transfer of an inhibitory tag of previously searched locations (inhibition of return; IOR) into retinal spatial reference frames (Sapir et al., 2004). Here we found both, facilitatory priming at previous target and inhibitory priming at previous distractor locations in retinotopical coordinates.

However, comparing the magnitude of facilitation and inhibition by comparing the average values of relative facilitation (M = 6.13 %; SD = 3.67) and relative inhibition (M = 2.54 %; SD = 3.43) revealed a strong tendency towards a statistical difference between the two values ($t(9) = 2.26$; $p = .05$). Comparisons between the "retinotopic experiment" (2) and the "control experiment" (1) were calculated. Facilitation found in retinal equal locations in the "retinotopic experiment" (2) was, although slightly weaker, statistically comparable ($t(18) = -2.00$; $p > .05$) in size to facilitation under static viewing conditions in the "control experiment" (1). However, inhibition was highly significantly weaker ($t(18) = 4.67$; $p < .01$) in the "retinotopic experiment" (2) than in the "control experiment" (1).

Basically we found facilitation and inhibition post-saccadically in retinotopical coordinates but effects were not as balanced as they were in the "control experiment" (1). Inhibition in the "retinotopic experiment" (2) was somewhat weaker compared to facilitation in the same experiment, and it was substantially diminished compared to the "control experiment" (1).

In the "spatiotopic experiment" (3) we tested whether we would find facilitation and inhibition in spatiotopic coordinates after saccades, and whether facilitation and inhibition would be affected differentially by overt attention shifts.

5. SPATIOTOPIC EXPERIMENT (3)

5. 1 Method

5. 1. 1 Participants

10 observers (5 male, mean age 24.7; *SD* = 16.32) with normal or corrected-to-normal visual acuity participated in the experiment. All subjects gave informed consent to participate in the study.

5. 1. 2 Materials

Stimuli were basically the same as in the "control experiment" (1) with the exception that the fixation cross was presented peripherally (8.2° of visual angle) in turns, on the left and on the right side of the search array (see figure 9).

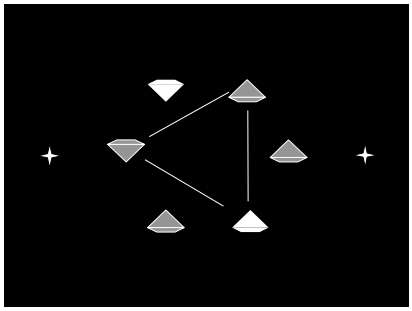


Figure 9. *The fixation cross was presented either on the left or on the right side of the screen, with switching side from trial to trial. Centrally, the search array was presented.*

5. 1. 3 Procedure

Task and procedure equalled basically the other experiments, with the difference to the "control experiment" (1) that a saccade was required subsequently to each trial in order to re-fixate on the (in turns from left to right and from right to left) switching fixation cross (see figure 10) and the difference to the "retinotopic experiment" (2) that a central search array was viewed from the peripheral fixation cross. To prevent subjects from using another strategy as the intended one, e. g. viewing the visual search array from a central eye position, subjects

were trained on the correct execution of saccades (in turns from the left to the right and from the right to the left sided fixation cross) during the 98 practise trials, preceding the experimental trials. During the experimental trials, correct re-fixations were controlled online by the experimenter via a mirror.

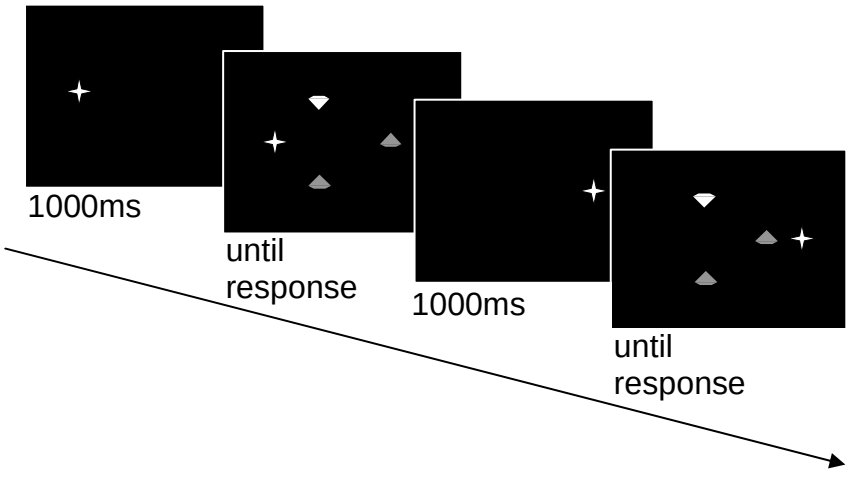


Figure 10. *A fixation cross was presented, in turns on the left and on the right side, followed by the visual search array in the centre, displaying the red target (depicted at white diamond) and two green distractor stimuli (depicted as gray diamonds).*

5. 2 Results and discussion

The same analyses were calculated as in the previous experiments.

Reaction times

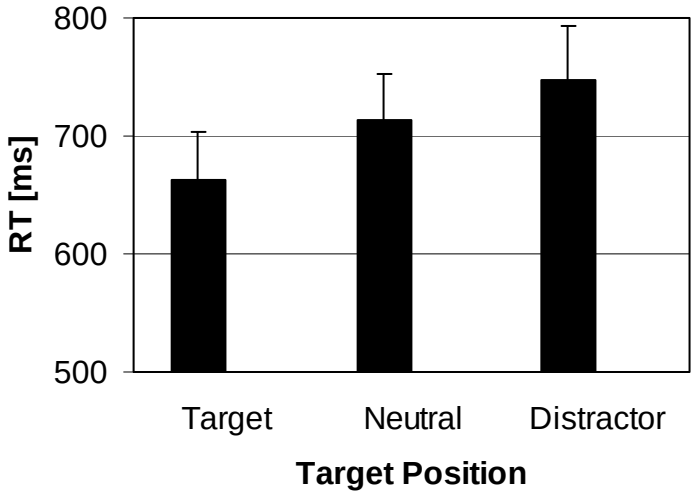


Figure 11. *Mean Reaction times (RTs) at the three target positions (target, neutral, and distractor). Error bars indicate standard errors.*

The ANOVA for RTs (as depicted in figure 11) revealed the main effect of Target Position to be highly significant [$F(2, 8) = 12.03$, $p < .01$]. RTs at previous target positions were highly significantly lower ($t(9) = -3.55$; $p < .01$), while RTs at previous distractor positions were significantly higher ($t(9) = -2.60$; $p < .05$) compared to RTs at neutral positions, indicating facilitation and inhibition.

Accuracy

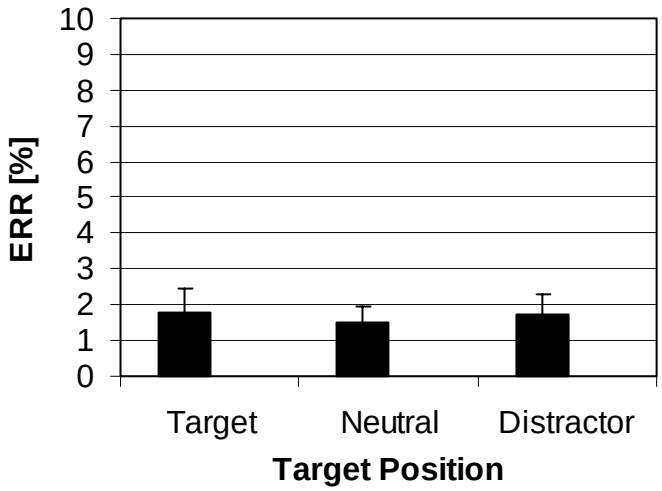


Figure 12. *Error percentage rates (err%) at the three target positions (target, neutral, distractor). Error bars indicate standard errors.*

Err% (as depicted in figure 12) were again low ($M = 1.66\%$; $SD = 1.46$) and comparable to err% in the previous experiments (difference non-significant; $p > .75$). The ANOVA revealed no significant main effect of Target Position ($p > .85$).

RTs revealed location priming to be present in spatiotopically equal locations after overt shifts of spatial attention. Basically, as indicated by relative facilitation ($M = -7.33$ %, $SD = 6.71$) and relative inhibition (M = 4.77, $SD = 5.52$), both priming effects were comparable in size to the effects found in the “retinotopic experiment” (2) at retinotopically equal locations. Analogously, magnitude of facilitation was comparable in size to facilitation found in the “control experiment” (difference non-significant; $p > .35$) whereas inhibition was significantly

diminished in the present “spatiotopic experiment” (3) compared to inhibition in the “control experiment” ($t(18) = 2.51$; $p < .05$).

In order to have time to present distracting stimuli in-between trials, a longer ISI was needed in the experiments 5 and 6.

Adjusted for that purpose, the “long-ISI-control experiment” (4) was implemented. It resembled the control experiment (1) with the exception of a prolonged ISI. With an ISI of 2,100 ms it was directly comparable to the upcoming experiments 5 and 6, which presented peripheral distractor stimuli in-between the trials.

6. LONG-ISI-CONTROL EXPERIMENT (4)

6. 1 Method

6. 1. 1 Participants

10 observers (5 male, mean age 31.8; *SD* = 13.78) with normal or corrected-to-normal visual acuity participated in the experiment. All subjects gave informed consent to participate in the study.

6. 1. 2 Materials

Stimuli were the same as in the "control experiment" (1).

6. 1. 3 Procedure

The procedure and task resembled the "control experiment" (1) with the exception that the ISI was 2,100 ms instead of 1,000 ms long.

6. 2 Results and discussion

The same analyses were calculated as in the previous experiments.

Reaction times

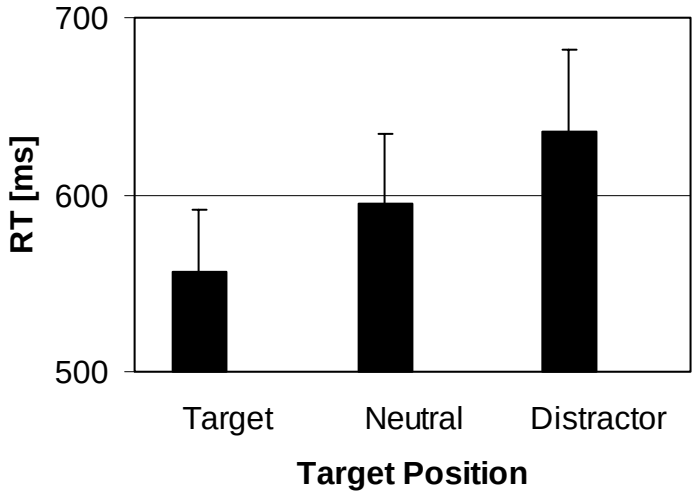


Figure 13. *Mean Reaction times (RT) at the three target positions (target, neutral, and distractor). Error bars indicate standard errors.*

The ANOVA revealed the main effect of Target Position to be significant. [$F(2, 8) = 25.25$, $p < .01$]. RTs (as depicted in figure 13) at previous target positions were significantly lower ($t(9) = -5.28$; $p < .01$), while RTs at previous distractor positions were significantly higher ($t(9) = -4.26$; $p < .01$) compared to RTs at neutral positions, indicating facilitation and inhibition.

Accuracy

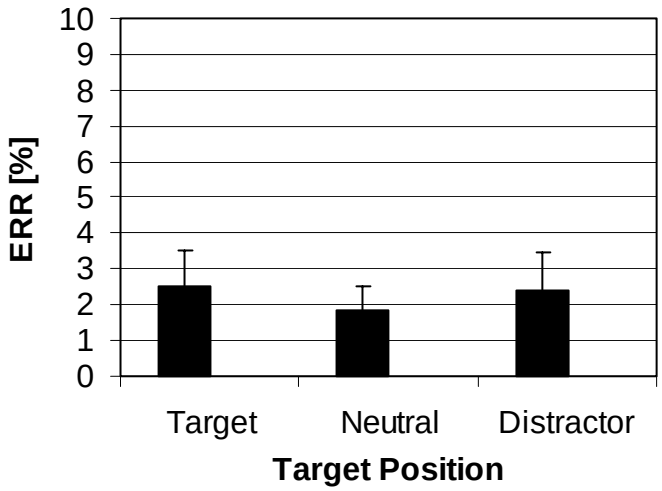


Figure 14. *Error percentage rates (err%) at the three target positions (target, neutral, distractor). Error bars indicate standard errors.*

The err% (as depicted in figure 14) were again low and did not differ from the err% in previous experiments ($p > .80$). The ANOVA revealed no differences at the different target positions (non-significant main effect of Target Position; $p > .60$).

Results of the RTs revealed analogously to the "control experiment" (1) facilitation and inhibition to be present. Furthermore relative facilitation ($M = 6.22$; $SD = 3.07$) was comparable in magnitude to relative inhibition ($M = 6.38$; $SD = 4.14$).

The influence of the prolonged ISI was investigated by comparing priming effects of the "control experiment" (1) and the "long ISI control experiment" (4). We found a strong tendency towards significantly reduced facilitation and inhibition (both ps $< .06$) in latter experiment. The prolonged ISI used in the "long ISI control experiment" (4) modulated the size

of facilitation and inhibition in a balanced way, i.e. both effects were diminished to the same extent.

Experiment 5 and 6 were designed to measure priming effects after covert attention shifts. Peripheral distractor stimuli were flashed in-between trials randomly on the left and the right side of the screen in order to distract attention covertly. Two different mechanisms are supposed to underlie spatial shifts of covert attention. That is, reflexive orienting towards exogenous visual stimuli and voluntary orienting towards endogenous stimuli (Müller & Rabbitt, 1989).

In the “irrelevant distractor experiment” (5) subjects were instructed to ignore the peripherally flashed distractors. However, it has been shown that reflexive orienting towards exogenous stimuli is automatic and not voluntarily suppressible (Jonides, 1981; Müller & Rabbitt, 1989). Hence, the peripheral distractors in the “irrelevant distractor experiment” (5) were supposed to activate reflexive orienting after each trial, although they did not have a task-related purpose such as e.g. predicting the spatial location of the target stimulus.

7. IRRELEVANT DISTRACTOR EXPERIMENT (5)

7. 1 Method

7. 1. 1 Participants

The same 10 observers as in experiment 4 participated in the experiment.

7. 1. 2 Materials

Stimuli were basically the same as in experiment 1. Additionally, peripheral visual inter-trial distractors (0.5° x 0.5° in size and 13.7cd/m^2 in luminance), were presented, randomly either 12.18° of visual angle to the left or to the right of the fixation cross, within the same horizontally level as the fixation cross (s. figure 15).

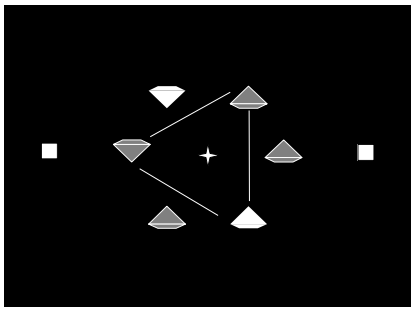


Figure 15. *Peripherally presented distractor stimuli were presented randomly on the left or on the right side. The search array was presented around the centred fixation cross.*

7. 1. 3 Procedure

The procedure and task resembled basically the procedure of the "long ISI control experiment (4) with the peripheral distractor being flashed for 100 ms after 600-800 ms during that interval (see figure 16). Participants were instructed to ignore the flashing distractor stimuli.

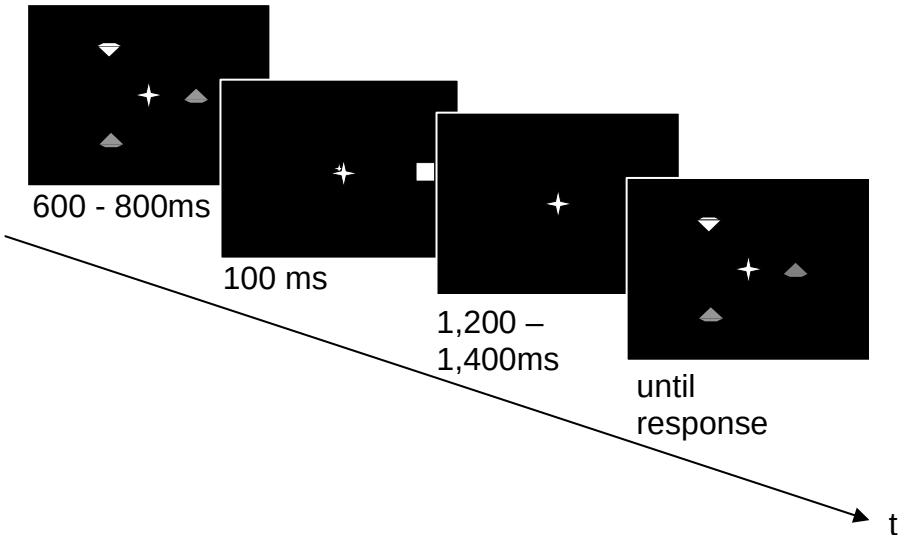


Figure 16. *A centred fixation cross was presented, followed by the visual search array around the fixation cross, displaying the red target (depicted as white diamond) and two green distractor stimuli (depicted as gray diamonds). Visual distractor stimuli were flashed randomly in the left or right periphery between the trials.*

7. 2 Results and discussion

The same analyses were calculated as in the previous experiments.

Reaction times

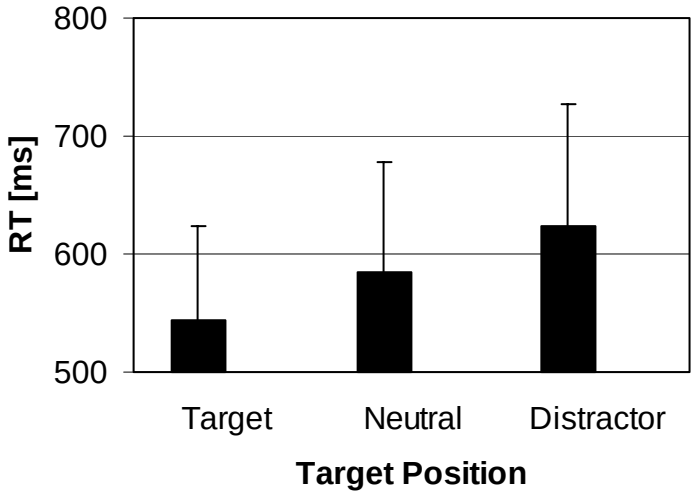


Figure 17. *Mean Reaction times (RT) at the three target positions (target, neutral, and distractor). Error bars indicate standard errors.*

The ANOVA revealed the main effect of Target Position to be significant. [$F(2, 8) = 35.84$, $p < .01$]. RTs (as depicted in figure 17) at previous target positions were significantly

lower ($t(9) = -5.97$; $p < .01$), while RTs at previous distractor positions were significantly higher ($t(9) = -5.64$; $p < .01$) compared to RTs at neutral positions, indicating facilitation and inhibition.

Accuracy

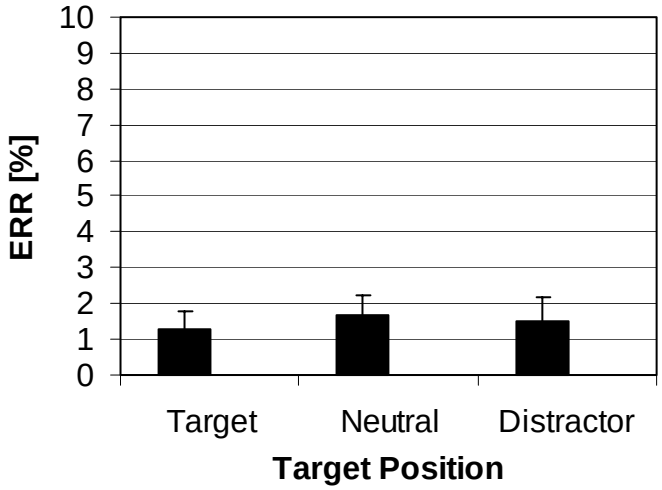


Figure 18. *Error percentage rates (err%) at the three target positions (target, neutral, distractor). Error bars indicate standard errors.*

The err% (as depicted in figure 18) were low and comparable to the previous experiments (non-signficant difference, $p > .85$). The ANOVA revealed no significant main effect of Target Position ($p > .85$).

The RTs at the different target positions revealed relative facilitation ($M = 6.75$ %, $SD = 3.17$) and inhibition ($M = 6.64$ %, $SD = 3.49$), to be equal in size compared to each other. The comparison of facilitation and inhibition between the "long-ISI-control experiment" (4) and the "irrelevant distractor experiment" (5) revealed no differences, concerning neither the magnitude of facilitation ($p > .70$) nor inhibition ($p > .85$), hence priming effects were comparable in the "long-ISI-control" and the "irrelevant distractor" experiment.

The peripherally flashed distractors in the "irrelevant distractor experiment" (5) were purely exogenous. In the "relevant distractor experiment" (6), we investigated whether facilitation and/or inhibition would be affected by covert attention shifts which are induced by

peripherally flashed distractor stimuli with an adherent endogenous component. The “relevant distractor experiment” (6) was alike the “irrelevant distractor experiment” (5) with the exception that a secondary task was conjoint with the peripheral distractors, inducing the endogenous component.

8. RELEVANT DISTRACTOR EXPERIMENT (6)

8. 1 Method

8. 1. 1 Participants

The same 10 observers as in experiment 4 and 5 participated in the experiment.

8. 1. 2 Materials

Stimuli were the same as in the “irrelevant distractor experiment” (see figure 15).

8. 1. 3 Procedure

Procedure and task were the same as in the “irrelevant distractor experiment” (5), with the exception that the peripheral distractors were relevant for a secondary task. Subjects had to indicate verbally the side (“left” or “right”) where the distractor had been flashed (s. figure 16).

8. 2 Results and discussion

The same analyses were calculated as in the previous experiments.

Reaction times

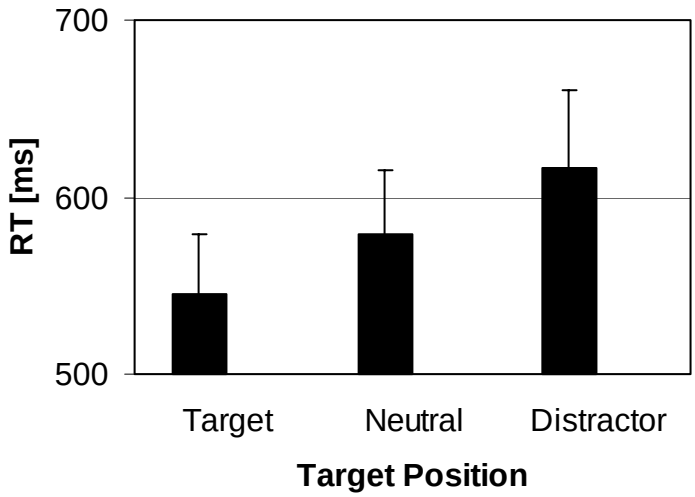


Figure 19. *Mean Reaction times (RT) at the three target positions (target, neutral, and distractor). Error bars indicate standard errors.*

The ANOVA revealed the main effect of Target Position to be significant. [$F(2, 8) = 28.33$, $p < .01$]. RTs (as depicted in figure 19) at previous target positions were significantly lower ($t(9) = -6.74$; $p < .01$), while RTs at previous distractor positions were significantly higher ($t(9) = -4.09$; $p < .01$) compared to RTs at neutral positions, indicating facilitation and inhibition.

Accuracy

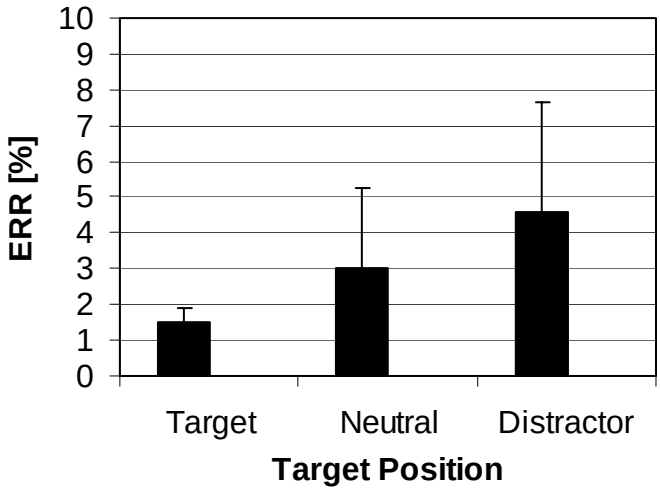


Figure 20. *Error percentage rates (err%) at the three target positions (target, neutral, distractor). Error bars indicate standard errors.*

Err% (as depicted in figure 20) were comparable to err% in the previous experiments ($p > .40$). However, the ANOVA revealed the main effect of Target Position to be significant. [$F(2, 8) = 6.88$, $p < .01$]. Err% at previous target positions were significantly lower ($t(9) = -2.02$; $p < .01$), while err% at previous distractor positions were significantly higher ($t(9) = -2.19$; $p < .01$) compared to err% at neutral positions, indicating facilitation and inhibition. Note, that although distribution of err% in the control (1) and the retinotopic experiment (2) followed a similar tendency, differences at the respective target positions did not reach significance level.

Here, facilitation at previous target positions and inhibition at previous distractor positions was reflected by both, errors and RTs. Although there was no difference in overall err% of all experiments err% of the present experiment as the only one out of all experiments differed significantly at the three possible kinds of target positions. This might reflect the higher demand of the secondary task required in the "relevant distractor experiment" (6).

RTs revealed facilitation and inhibition in an analogous way as accuracy did. Facilitation and inhibition did not differ in magnitude ($p > .80$), i.e. they were balanced. Also, no differences between facilitation and inhibition compared to the respective values in the "long-ISI-control experiment" (both ps > .80) or to the "irrelevant distractor experiment" (both ps > .50) were found.

In the "relevant distractor experiment" (6) a secondary task conjoint with peripherally flashed distractors required subjects to shift spatial covert attention voluntarily (endogenously). Both, facilitation and inhibition were balanced and robustly present, and comparable in magnitude to priming effects in the "long-ISI-control experiment". Hence, performance of the primary (visual search) task was not affected by endogenous covert shifts of attention. On the contrary, – although overall err% did not differ significantly from the rates of all other experiments – its distribution was modulated by the respective target positions. In particular, the likelihood to perform correctly at locations which where attended before (previous target positions) and the likelihood to commit an error at locations which had been previously ignored (previous distractor positions) was significantly increased. In this aspect the result of the present experiment differed from the results of the "long-ISI control experiment" (4) and the "irrelevant distractor experiment" (5).

9. CONCLUSION

We investigated the effects of spatial attention shifts on location priming. Facilitation and inhibition are considered to basically reflect mechanisms which operate to support visual search. In particular, they indicate integration of previous visual information into current visual search, thus visual search does not start anew with each eye fixation but benefits from previous experience. Because visual search normally takes place in dynamic surroundings which requires lots of shifts of attention to adapt to given situations constantly, we investigated impact of instability induced by overt and covert attention shifts.

We were interested in whether robust effects accompanying visual search under specific conditions (e.g. robust facilitation and inhibition within a certain arrangement of stimuli) outlive spatial shifts of attention, and if, whether, firstly overt and covert attention shifts would have a different impact on priming effects, and secondly, facilitation and inhibition would be affected differentially by our experimental modifications.

In the “control experiment” (1), we obtained robust facilitation and inhibition under static viewing conditions. We replicated results found in previous studies using priming of pop-out (Maljkovic & Nakayama, Geyer et al., 2007). In the “retinotopic” (2) and “spatiotopic experiment” (3) subjects were required to shift spatial attention overtly. Priming effects were measured post-sacadically at retinotopic (experiment 2) and at spatiotopic (experiment 3) locations. We found them present at both locations, with the impact on facilitation and inhibition equal in both experiments. Compared to the “control experiment” (1) magnitude of facilitation was somewhat diminished but statistically comparable in the “retinotopic” (2) and “spatiotopic experiment” (3), respectively. Magnitude of inhibition however was significantly diminished in the “retinotopic” (2) and “spatiotopic experiment” (3), respectively, compared to the “control experiment” (1).

The results of the “retinotopic” (2) and “spatiotopic experiment” (3) suggest an equal impact of overt attention on location priming regardless in which spatial reference system

effects are measured. However, saccades seem to have a differential impact on facilitation and inhibition, respectively. This is in accordance with the assumption that facilitatory and inhibitory priming effects reflect two different mechanisms to sub-serve different components in visual search (Geyer et al., 2007). Inhibition but not facilitation was affected by the set size (i.e. the number of distractors presented along with a target stimulus in a search array). In particular it was virtually not present with set sizes exceeding the number of two distractors (Geyer & Müller, submitted). Furthermore, Geyer et al. (2007) demonstrated that facilitation relies to some extent and inhibition relies entirely on the regularity of stimulus arrangements. Recently, Finke, Bucher, Kerkhoff, Keller, von Rosen, Geyer, Müller, & Bublak (in press) showed that inhibition but not facilitation was affected in two patients with lesions to the right frontal eye fields. In line with studies which support the notion that inhibition is less robust than facilitation (Maljkovic & Nakayama, 1996) by revealing factors that affect inhibition but not facilitation we found a forfeit for facilitation to some extend but a more substantial forfeit for inhibition after overt shifts of attention. However, basically, we showed that priming effects outlive saccades and are post-saccadically measurable in both retinotopic and spatiotopic coordinates. The spatial transfer could have been accomplished by remapping mechanisms (Gottlieb, 2007) in the same way as features, form, and motion (Melcher & Morrone, 2003; Melcher, 2005) or even mechanisms operating in visual search such as IOR (Sapir et al., 2004) had been found to be remapped into retinotopical and spatiotopical coordinates.

Prior to the investigation of overt attention shifts on location priming – in order to provide an appropriate condition for comparisons for experiments 5 and 6 - we replicated the results of facilitation and inhibition in the “long-ISI-control experiment” (4). The effect attributable to the longer ISI was a marginally significant equable decline of facilitation and inhibition as compared to the “control experiment” (1). In the “irrelevant distractor” (5) and “relevant distractor experiment” (6) we investigated spatial covert attention shifts induced by exogenously reflexive and endogenously voluntarily orienting (Müller & Rabbitt, 1989),

respectively. Facilitatory and inhibitory priming effects were present in both experiments. Results suggest complete outliving of priming after either of the induced covert attention shifts. Firstly, magnitudes of facilitation and inhibition were equally balanced. Secondly, in both experiments, facilitation and inhibition were comparable in magnitude to the respective effects in the "long-ISI-control experiment" (4) and among each other. Moreover, in the "relevant distractor experiment" (6) facilitation and inhibition was additionally reflected by the err%.

According to findings suggesting a fronto-parietal neural network underlying covert attention shifts which is – in large part - shared by reflexive and voluntary mechanisms driving covert attention (Nobre, Sebestyen, Gitelman, Mesulam, Frackowiak et al., 1997; Rosen, Rao, Caffarra, Scaglioni, Bobholz, et al., 1999; Peelen, Heslefeld, & Theeuwes, 2004) we found a similar impact of reflexive (exogenous) and voluntary (endogenous) covert attention shifts on location priming. However, we found expansion of priming effects on accuracy selectively in the "relevant distractor experiment" (6). Endogenous shifts are known to be less automatic and more effortful which is reflected by an enhanced activation of the neural network compared to exogenous shifts (Rosen et al., 1999). Furthermore selective activation of right dorsolateral prefrontal structures in endogenous but not exogenous shifts suggests the engagement of working memory in tasks which involve voluntary covert attention shifts (Rosen et al., 1999). Corbetta, Kincade, & Shulman (2002) found the fronto-parietal network involved in endogenous shifts of attention also involved in spatial working memory. Based on findings which distinguish exogenous and endogenous mechanisms driving covert attention shifts, the distinctive finding of facilitation and inhibition being additionally reflected by accuracy in a task involving endogenous ("relevant distractor experiment") as compared to a task involving exogenous covert attention shifts ("irrelevant distractor experiment") might either reflect greater effort or involvement of spatial working memory in the "relevant distractor experiment" (9). In either case, the higher demand became evident as an expansion of priming effects to performance accuracy.

Despite common underlying neural mechanisms (Nobre et al., 2000; Beauchamp et al., 2001) and functional overlap (e. g. Deubel & Schneider, 1996) of overt and covert attention, we found an impact of covert attention shifts on location priming effects which differed from the impact of overt attention shifts. In particular, we found a modulation of priming after overt but not after covert shifts of attention. Similar differences between overt and covert shifts of attention have been found in studies showing that perception in an invariant-object recognition task (Cox et al., 2005) and a form adaptation task (Melcher, 2007) was affected by overt but not by covert attention shifts. Also there is evidence that parietal neurons in monkeys do not specifically discharge in response to new locations after covert but after overt attention shifts (Duhamel et al., 1992b).

Our results suggest two different ways of "outliving" overt and covert attention shifts for location priming, respectively. Priming effects seemed to have outlived overt shifts by being spatially remapped into post-saccadic coordinates which was reflected by some "costs" as indicated by a somewhat smaller facilitation and a significantly decreased inhibition effect. In contrast, priming effects seemed to have outlived covert shifts by protection against irrelevant ("irrelevant distractor experiment") and relevant distraction ("relevant distractor experiment"). As indicated by the results of the latter experiment, voluntary shifts of covert attention in order to perform a secondary task at a different spatial location did not affect priming effects reflected by RTs but – on the contrary – led to an extension of priming by enclosing accuracy. This might be interpreted as additional support by location priming which came into play in order to support keeping track with the primary (visual search) task along with an attention demanding secondary task.

In conclusion, the finding of outliving (or even expanding) location priming effects after shifts of overt and covert attention provides evidence for the crucial role of location priming in visual search in dynamic environments.

III. CHAPTER

STUDY 2

ARE THERE SACCADIC SPATIAL REMAPPING DEFICITS IN PATIENTS WITH RIGHT PARIETAL LESIONS?

1. Abstract

Spatial remapping processes are supposed to operate in order to integrate subsequently presented visual information. Their integrity is a prerequisite to compensate for changes in a dynamic environment and self-movements such as saccades. Furthermore, deficient spatial remapping mechanisms might contribute to visual search impairments in patients with right parietal lesions (Pisella & Mattingley, 2004), such as repeated search of previously searched locations (Husain, et al., 2001; Pisella, Berberovic, & Mattingley, 2004; Mannan, Mort, Hodgson, Driver, Kennard et al., 2005;) or a failure of using previously provided visual information on current visual scenes (Shimozaki, Hayhoe, Zelinsky, Weinstein, Merigan, et al., 2003). The integrity of spatial remapping is indicated by location-based facilitation and inhibition in a priming of pop-out paradigm (Maljkovic & Nakayama, 1996; Chun & Nakayama, 2000). To analyse spatial remapping deficits we investigated location priming in patients with right-sided lesions with (PAR) and without parietal (NONPAR) involvement and in age and education-matched healthy subjects (CON) in three experiments. First, the "control experiment" (7) with retinotopically equal subsequent visual search displays. Second, the "saccade experiment" (8), requiring saccadic eye movements between the trials but nevertheless presenting subsequent visual search displays retinotopically equal, thus requiring no spatial remapping, and third, the "spatial remapping experiment" (9), requiring spatial remapping due to alternating gaze positions between subsequent trials.

In the "control" (7) and the "saccade experiment" (8), without spatial remapping requirements, all groups showed priming effects, with facilitation even enhanced in the "control experiment" (7) in the PAR group. In the "spatial remapping experiment" (9), NONPAR and CON group showed priming effects. However, location priming was completely extinguished in the PAR group, indicating deficient spatial remapping mechanisms after right parietal lobe lesions. Implications of spatial remapping deficits on visual search impairments following right parietal lesions are discussed.

2. Introduction

A basic prerequisite for orienting and acting in space properly is the continuous updating of a spatial representation of the environment with which one interacts. Subjectively experienced as a coherent and stable entity, space - rather than being encoded in a topographical map which represents “real” space - actually is encoded in multiple spatial reference frames with information provided in a multimodal manner to guide visual search and behaviour (Pouget & Sejnowski, 1997).

A brain region crucial for constructing and representing space is the parietal cortex (Pouget & Driver, 2000), in particular, the posterior parietal cortex (PPC; Sereno et al., 2001) with a number of functional distinctive areas (see Colby & Goldberg, 1999 for a review). Anatomically located between visual, auditory, and somato-sensory areas, the PPC has been suggested to function as an interface between sensory perception and motor output (Andersen, 1999; Linden, Grunewald & Andersen, 1999; Grunewald, Linden & Andersen, 1999). Input from the different sensory modality areas (visual, auditory, somatosensory) converge with vestibular (Karnath Fetter, & Dichgans, 1996; Andersen, Snyder, Batista, Buneo & Cohen, 1999; Ventre-Dominey & Vallee, 2006) and proprioceptive (Fasold, Heinau, Trenner, Villringer & Wenzel, 2008) information to construct impressions of space. Visual input which is depicted retinotopically must be transformed into representations which contain spatial information. Crucial for constructing a reliable internal visual representation of a dynamic external environment is the distinction between and the compensation for movements in the environment and self-movements, and the updating of the representations along with these changes (Medendorp, Smith, Twee, & Crawford, 2002; Rushworth & Taylor, 2006). Seamless spatial representation of the environment requires the spatio-temporal integration of contents of single eye fixations which are, on the retinal level, overwritten along with each new fixation (Jonides, Irwin, & Yantis, 1982; O´Regan & Lévy-Schoen, 1983). This

integration process has been suggested to be accomplished by spatial remapping mechanisms (Colby, et al., 1995; Pisella & Mattingley, 2004).

In monkeys, neurons of the lateral intraparietal cortex (LIP) in the PPC were found to compensate for saccadic eye movements in order to process a stimulus in a spatially accurate manner after a saccade by exhibiting predictive or memory-based remapping, i.e., they discharge before an upcoming saccade brings a visual target stimulus into their receptive fields (Duhamel, et al., 1992b; Bays & Husain, 2007); or respond to a visual memory trace of a target stimulus which has been remapped in conjunction with an eye movement (Duhamel, et al., 1992b; Heiser, Berman, Saunders, and Colby, 2005; Berman, Heiser, Dunn, Saunders, and Colby, 2007). Hence, characteristic behaviour of its neurons qualifies area LIP in monkey to be a candidate for a neuronal substrate of spatial remapping. In humans, the contralateral superior parietal cortex has been found to map space and was suggested as a homologue of monkey's area LIP (Stein, 1989; Sereno, et al., 2001). In line with this view, studies using brain imaging (Merriam, Genovese, & Colby, 2003), electrophysiological (Bellebaum Hoffmann, & Daum, 2005; Bellebaum & Daum, 2006), and transcranial magnetic stimulation techniques (TMS; Chang & Ro, 2007; Morris, Chambers, & Mattingley, 2007) also suggest the human PPC to provide an anatomical correlate of spatial remapping. Consistently, Farrell and Robertson (2000) reported impaired updating of environmental representations in patients with PPC lesions.

However, little is known about how spatial remapping mechanisms operate in humans (Morris et al., 2007). Pisella and Mattingley (2004) proposed a model according to which spatial remapping mechanisms ensure spatio-temporal contingency between successive retinal images by constantly updating representations of visual information on a saliency map (Itti & Koch, 2001). Information which is represented most saliently on the map is selected subsequently for conscious representation by the allocation of covert and overt attention (Niebur & Koch, 1998; Itti & Koch, 2001). After the most salient stimulus has been selected,

activity on the saliency map at the selected location is suppressed and attention is re-allocated to the location of the next-highest salient stimulus on the saliency map and so on (Itti 2000). A stable construct of the environment evolves from constant (re-)allocation of attention to locations of salient stimuli.

According to Pisella and Mattingley (2004), deficient spatial remapping mechanisms following parietal lesions lead to an overwriting of visual information on the saliency map along with each new ocular fixation, and thus prevent establishing of stable spatial arrays. Successive retinal images are no longer integrated across space and time. The authors suggest this lack of spatio-temporal continuity to contribute to a number of characteristic visual search impairments reported in patients with parietal lesions.

In the following we summarise visual search impairments found in those patients against the background of the model and come up with a method to test some of the model's assumptions.

Well established to investigate spatial remapping abilities is the double-step saccade task (Becker & Jürgens, 1979; Tobler, Felbinger, Bürki, Nirkko, Ozdoba, et al., 2001; Heide, Binkofski, Seitz, Posse, Nitschke et al., 2001; Sommer & Wurtz, 2002). Two subsequent saccades to two targets which disappear after having been flashed briefly have to be conducted. Targets are not visible throughout the performance of the task. While the first saccade is guided by retinotopical representation, the correct execution of the second saccade requires the updating of the visual scene after re-calculating the new starting point for the second saccade from the landing point of the first saccade, i.e. the first target. Patients with right parietal lesions perform inaccurate second saccades, interestingly only when the first saccade is conducted towards the contralesional (left) hemi-field (Duhamel, et al., 1992a; Heide, et al., 1995). Morris et al. (2007) were able to replicate these findings by applying TMS over the right intraparietal sulcus in healthy observers.

The assumption made by Pisella and Mattingley (2004) according to which after right parietal lesions leftward saccades lead to overwriting of information on the whole saliency map while rightward saccades merely lead to overwriting of information on the left side of the saliency map, could account for saccade-direction specific findings in the double-step saccade task.

Husain et al. (2001) examined the visual search pattern across saccades in a patient with neglect following a focal right parietal lesion. In a cancellation task, that required looking for a target item among distractors, the patient ignored stimuli on the left side, and interestingly, re-fixated stimuli on the right side frequently. This "revisiting behaviour" often reported in patients with parietal lesions (Eglin & Robertson 1989; Wojciulik, et al., 2001; Pisella et al., 2004; Mannan et al., 2005) might also arise from a failure of spatio-temporal integration of previous visual information. In particular, in intact visual search, previous visual information brings about the marking of previously searched locations with inhibitory tags (Shore & Klein, 2001) in order to support advancement of the search towards not yet explored stimuli (Klein, 1988; 2000). In the presence of remapping deficits helpful mechanisms accompanying visual search might be absent and not remapped due to the overwriting of information on the level of the saliency map. Sapir, et al., (2004) approached exactly this issue by investigating remapping of IOR across saccades. IOR is an inhibitory tag accompanying visual search in order to enhance smooth performance (Posner & Cohen, 1984; Klein, 2000). Sapir et al. (2004) found healthy subjects to remap IOR after a saccade in both, retinotopical and environmental coordinates. In patients with lesions to the intraparietal sulcus, IOR was only present in retinotopical coordinates, indicating that IOR was not remapped, thus environmental representation was not updated along with saccades.

Another impairment of exploration behaviour in patients with parietal lesions concerns the use of previous spatial information in order to facilitate processing of targets at certain locations. Shimozaki et al. (2003) demonstrated the inability of patients with parietal lesions

to benefit from previously provided information about target locations by preview displays in a current trial. Naturalistic scenes were shown in preview displays, followed by a display that showed the target item for which to look for in a proximately upcoming search display which equalled the preview display. While healthy subjects were able to detect the target at the respective location immediately and made a goal-directed saccade towards it, patients showed a random search pattern, clearly suggesting that they did not benefit from previously provided information. Presumably, and in accordance with Pisella and Mattingley´s (2004) assumptions, healthy subjects were able to integrate subsequently presented visual information by successful remapping of preview and search display representations on the saliency map. Equality of preview and search display was easily recognised despite the intermittent presentation of the target indicating display which provided a spatial remapping requirement. However, in the case of deficient spatial remapping abilities as assumed to be present in patients with parietal lesions, the integration of sequentially presented information might have failed since the spatial remapping requirement was not fulfilled.

In the present study we explicitly investigated the influence of previously presented visual information on performance in current trials in terms of facilitation and inhibition on target detection. To that end, we applied a priming of pop-out paradigm (Bravo & Nakayama, 1992; Maljkovic & Nakayama, 1996). Location based facilitatory and inhibitory priming effects were measured as a function of the preceding trial: Targets appearing at previous target locations are detected faster and more accurately (facilitation), while detection of targets at previous distractor locations is slower and more error-prone (inhibition). The presence of these cross-trial priming effects indicates successful spatio-temporal integration of subsequent visual images (Chun & Nakayama, 2000). We analysed location priming effects, and thus the ability to integrate visual information across sequential trials in three different experiments. In each experiment, two groups of right-hemispheric lesioned patients,

with and without parietal involvement, and a group of age- and education matched subjects participated, respectively.

In the “control experiment” (7) the visual search array was presented centrally around a central fixation cross, requiring neither saccades nor spatial remapping. As previously shown, location priming in visual pop-out search without spatial remapping requirements and unlimited presentation time of search displays similar to the task used in the “control experiment” (7) is preserved in neglect patients (Kristjánsson, Vuilleumier, Malhotra, Husain, and Driver, 2005). Complementary, preliminary results of the current study focused on both, facilitatory and inhibitory priming. While facilitatory priming was equally present in patients with neglect following right-hemispheric damage compared to healthy subjects inhibitory priming was shown to be present however slightly diminished, especially in two patients with lesions encroaching on the frontal eye fields (Finke, et al., in press). Hence, we expected location priming to be basically present in patients with parietal lesions in the “control experiment” (7). Albeit, Finke et al. (in press) provided evidence that facilitation and inhibition might be differentially affected in a task without spatial remapping.

Studies which demonstrated visual search impairments that can be interpreted as arising from an inability to spatio-temporally integrate visual information in patients with parietal lesions (Husain et al., 2001; Shimozaki et al., 2003) used tasks which required the patients to conduct saccades. Impairments resulting from saccade-related problems such as saccade planning or motor problems cannot be disentangled from spatial remapping deficits in those tasks. Here, we investigated pure impact of saccades on location priming. In the “saccade experiment” (8) the visual search array occurred around a fixation cross presented in turns on the left and on the right side of the screen, thus requiring saccades between sequential trials in order to re-fixate the fixation cross but no spatial remapping due to a search array, presented constantly in terms of egocentric and retinotopically equal coordinates. Based on previous findings such as saccadic remapping of IOR in retinotopical

coordinates (Sapir et al., 2004) and also evidence drawn from double step saccade tasks (accurate first and disturbed second saccade; Duhamel, et al., 1992a; Heide et al., 1995) we expected patients with parietal lesions to show preserved priming effects in the "saccade experiment" (8).

In the "spatial remapping experiment" (9) the visual search array was again centrally presented but was viewed from a peripheral fixation cross presented in turns on the left and on the right side of the screen (and the search array), requiring saccades between the trials in order to re-fixate the fixation cross, and additionally spatial remapping to compensate for the saccades. We expected priming effects to be attenuated or even absent in patients with parietal damage, since we assumed spatio-temporal integration of successive visual information after parietal damage to be disturbed. An absence of facilitation might contribute to explain why patients with parietal lesions showed no benefit from preview displays in terms of faster RTs to targets (Shimozaki et al., 2003). An absence of inhibition, an effect considered to reflect inhibitory tagging mechanisms in charge of enhancing search towards new locations (Maljkovic & Nakayama, 1996; Klein, 1988) might account for revisiting behaviour (e.g. Husain, 2001).

Priming effects are regarded as implicit – passive and automatic – memory mechanisms which helpfully accompany intact visual search (Chun & Nakayama, 2000; Shore & Klein, 2001). They are commonly measured across sequentially presented trials, in healthy subjects, and without the occurrence of disturbing events between subsequent trials like goal-directed saccades or the additional necessity to encode spatial arrays from different viewing perspectives, thus requiring spatial remapping between subsequent trials. Based on previous findings (Sapir et al., 2004, and study 1, II. chapter, p 22), and the assumption that priming is important for exploration in a dynamic environment, we expected priming effects to be still present after saccades in-between trials ("saccade experiment"). Furthermore, we expected priming to be remapped across space and time ("spatial remapping experiment") in

healthy subjects. Moreover, we expected that deficits of spatial remapping can be attributed to parietal lesions and thus are preserved in patients with lesions not involving the parietal lobe.

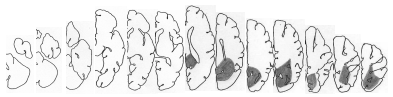
3. CONTROL EXPERIMENT (7)

3. 1 Method

3. 1. 1 Participants

Patients with right sided brain damage were recruited from a neurological rehabilitation clinic. They were assigned to either of two groups, on the basis of their injury location, with parietal involvement (PAR) or without parietal involvement (NONPAR) as documented by the reports of previous radiological examinations. The assignment was confirmed by a second validation of CT/MR scans at the point in time of testing (see figure 21). 15 PAR patients and 15 NONPAR patients took part in the "control experiment" (7). All gave written informed consent to participate in the study, according to the declaration of Helsinki II. Patients were tested at a median of 9 and within a range of 3 up to 500[2] weeks post injury. The patient groups did not differ significantly with respect to time since brain injury [$F(1, 28) = 1.50$; $p > .23$].

PAR:

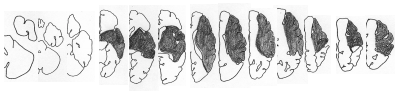
OD 

KF 

LH-L 

KW 

K-KL 

CH 

GS 

RL 

[2] As an exception, patient KW suffers from an old lesion since years. He was a former patient of a rehabilitation clinic, and was the first one tested, in the forefront of this study.

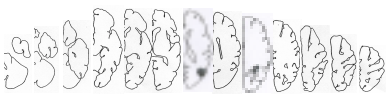
KH 

ML 

DR 

GZ 

MP1 

KL 

SW 

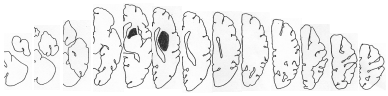
NONPAR:

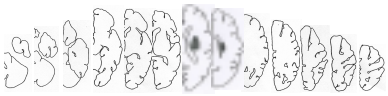
VS 

GR 

MK1 

AB 

HA 

MK3 

MM 

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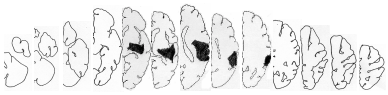
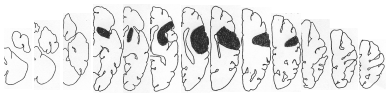
OB 

MK2 

MP2 

VC 

Figure 21. *Lesion reconstructions of the 30 patients. Lesions have been drawn onto standard slices from the Damasio template system (Damasio & Damasio, 1989). Only the affected right hemisphere is depicted.*
Abbreviations: PAR, group of patients with right-sided injury with parietal involvement; NONPAR, group of patients with right-sided injury without parietal involvement.

Patients with insufficient comprehension of instruction were excluded, as were patients with acute visual neglect, interfering with the perceptual requirements for the experimental task. Some of the patients with and without parietal lesions who participated in this study had had neglect after lesion onset. Although recovered in large part until the time of testing the patients might have suffered from mild neglect. Hence, the contingent contribution of neglect on the performance pattern was surveyed closely. Information about the presence of residual neglect symptoms are derived from standard diagnosis in the clinic.

The patient data were compared to the data of 15 age- and education matched control subjects (CON), who had no history of psychiatric or neurological disorder. Patient groups did not differ significantly from the CON group with respect to age [$F(2, 42) = .14$, $p > .85$] or education [$F(2, 42) = 0.75$, $p > .45$]. Demographical information is given in table 1.

Table 1

Group demographics and clinical information. Gender distribution, median and range for age, education, and time since injury, residual neglect

	sex (f/m)	Age [years]	education [years]	TSI [weeks]	Injury type (CVA/Tu)	Residual neglect
CON	7/8	54 (34 – 78)	10 (8 – 13)	-	-	-
PAR	3/12	51 (27 – 78)	10 (8 – 13)	15 (3 – 500)	15/0	11
NONPAR	5/10	52 (34 – 77)	12 (9 – 13)	7 (3 – 27.9)	14/1	5

Abbreviations: CON, healthy age and education matched control group

All patients and control subjects had either normal or corrected-to-normal visual acuity. Seven patients of the PAR group and two patients of the NONPAR group suffered from partial visual field loss as assessed by clinical standard diagnostic. Visual field defects

are depicted in figure 22. As assessed by a handedness-inventory, two patients (one of the PAR and one of the NONPAR group) and one control subject were left-handed.

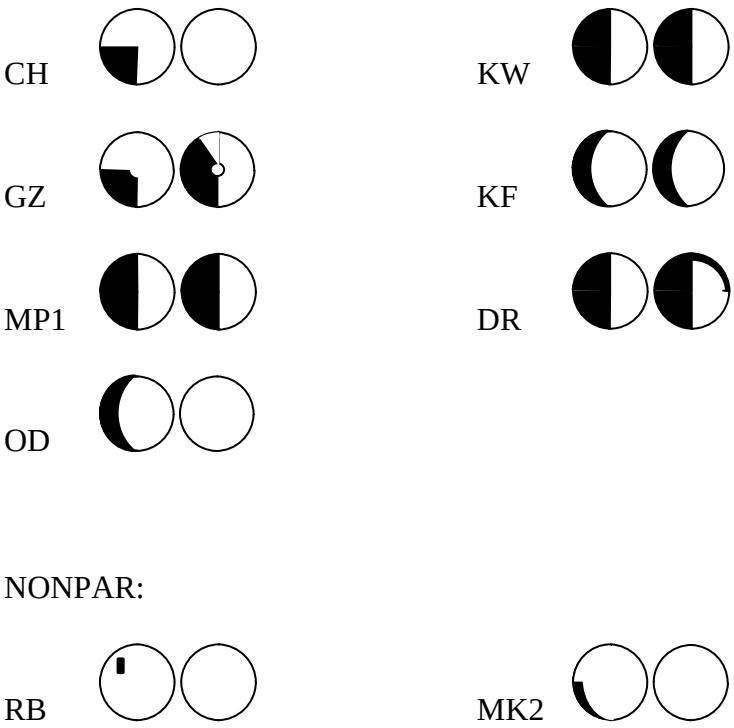


Figure 22. *Visual field defects of patients with (PAR) and without (NONPAR) parietal lobe lesions are depicted.*

3. 1. 2 Materials

Materials and stimuli were the same as in the "control experiment" (1) in study 1, II. chapter, p.28, in the present thesis. Note that no stimuli occurred on the imaginary vertical midline, permitting RTs and errors to be determined separately for the left and the right visual field (figure 23).

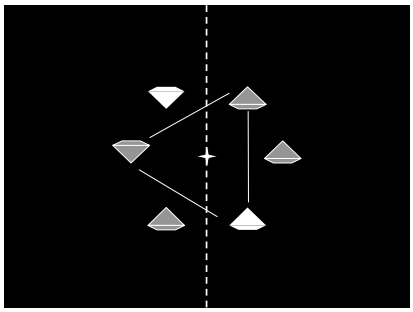


Figure 23. *Illustration of the search displays used in the "control experiment" (1). The red target (depicted as white diamond) appeared in either the left or right visual hemi-field together with two green distractors (depicted as gray diamonds). One possible search display is indicated by the connecting lines between the stimuli, another display is shown without connecting lines. No stimuli appeared on the imaginary vertical midline (illustrated by the dashed line).*

3. 1. 3 Procedure

Procedure was the same as in the "control experiment (1) in study 1, II. chapter, p. 28. RTs and errors were recorded for the left and right hemi-field, separately. If necessary, break durations between experimental blocks were adjusted to patients´ individual requirements.

3. 2 Results

The dependent variables RTs (excluding error trials and trials following an error trial, as well as extreme values 2 standard deviations above or beneath mean RTs of the respective target position) and accuracy (err%) were examined in separate ANOVAs with the between-subject factors Group (CON, PAR, NONPAR) and the within-subject factors Target Position (target at previous target location, at previous distractor location, at previously empty location) and Side (target in left, in right hemi-field). Level of significance was 5%.

Reaction times

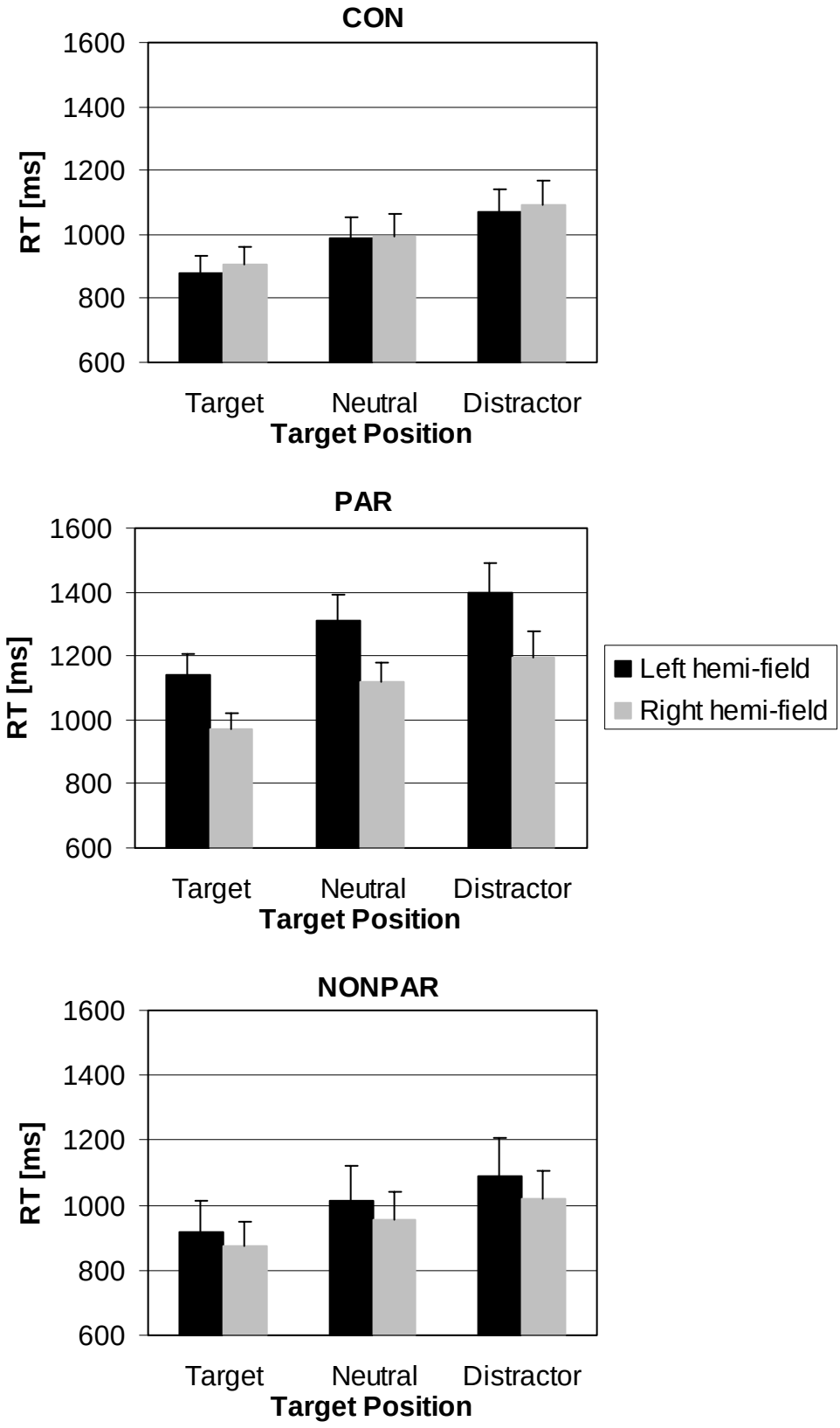


Figure 24. *Mean reaction times (RT) at the three target positions (target, neutral, and distractor) in the left and the right hemi-field for each group (CON, PAR, NONPAR), respectively are depicted. Error bars indicate standard errors.*

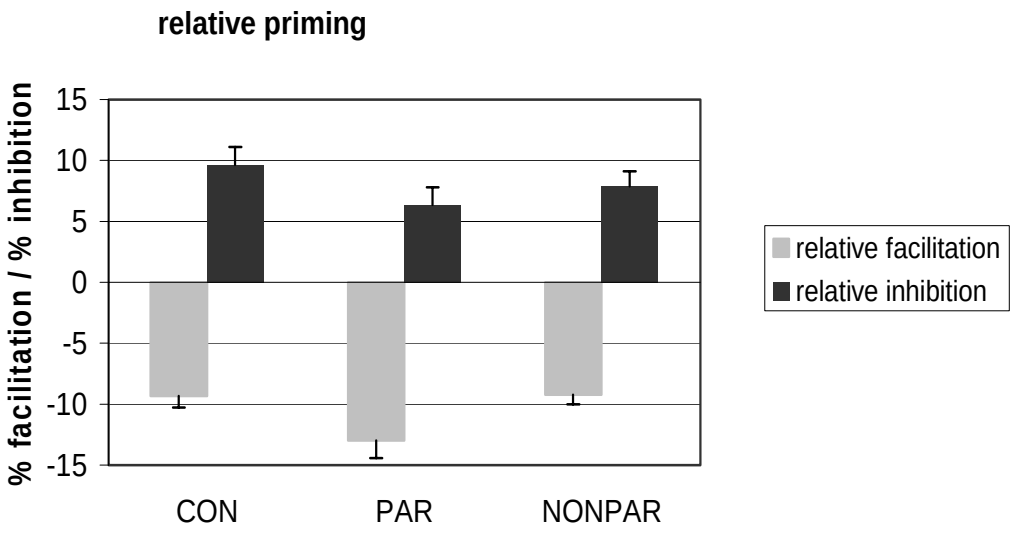


Figure 25. *Relative priming effects (facilitation and inhibition in percent) is depicted for each group (CON, PAR, NONPR), separately. Error bars indicate standard errors.*

Mean RTs for each group at the three target positions in the left and the right hemi-field, respectively are shown in figure 24.

The ANOVA revealed the main effects of Target Position [$F(2, 41) = 137.53$, $p < .01$] and Side [$F(1, 42) = 16.99$; $p < .01$] as well as the interactions Group × Target Position [$F(4, 84) = 2.52$; $p < .05$] and Group × Side [$F(2, 46) = 10.65$; $p < .01$] to be significant.

The main effect of Group showed a tendency ($p < .10$) towards significance.

In all groups, RTs at previous target positions were significantly lower (CON: $t(14) = -6.67$; $p < .01$; PAR: $t(14) = -7.21$; $p < .01$; NONPAR: $t(14) = -6.82$; $p < .01$), while RTs at previous distractor positions were significantly higher, (CON: $t(14) = -7.23$; $p < .01$; PAR: $t(14) = -3.94$; $p < .01$; NONPAR: $t(14) = -5.72$; $p < .01$) compared to RTs at neutral positions, indicating facilitation and inhibition. Comparing RTs at the target positions, respectively, across groups, t-test revealed that compared to CON group PAR group reacted significantly slower to targets at previous target positions ($t(28) = -2.13$; $p < .05$) and neutral positions ($t(28) = -2.37$; $p < .05$) but was comparable at previous distractor positions ($p > .05$). This indicates that priming effects in the PAR group were not balanced, that is, either that

compared to facilitation inhibition was slightly diminished or compared to inhibition facilitation was slightly more pronounced in the PAR group.

While PAR group patients responded significantly slower ($t(14) = 4.03$; $p < .01$) to targets in the left as compared to targets in the right hemi-field, healthy subjects at the most showed a tendency ($t(14) = -2.08$; $p < .06$) for the opposite, i.e. faster responses to targets in the left as compared to targets in the right hemi-field. Patients of the NONPAR group showed marginally significant higher RTs ($t(14) = 2.03$; $p < .07$) to targets in the left compared to targets in the right hemi-field.

The interactions of Side × Target Position, and Group × Target Position × Side were non-significant (all *p*s > .50).

To directly compare priming effects, we calculated the facilitation and inhibition effects relative to the overall RTs (in percent). Given that there was no significant Target Position × Side, facilitation and inhibition effects were calculated across both hemi-fields, respectively (see figure 25). One-way ANOVAs were used to test for differences of relative facilitation and relative inhibition in the three groups (CON, PAR, and NONPAR), respectively. Relative facilitation differed significantly across the groups [$F(2, 42) = 3.83$; $p < .05$], while relative inhibition was comparable across groups ($p > .25$). Relative facilitation in the PAR group was significantly more pronounced compared to the CON ($t(15) = 2.12$; $p < .05$) and the NONPAR group ($t(15) = 2.29$; $p < .05$). The CON and the NONPAR group did not differ significantly ($p > 90$).

Influence of neglect

16 out of 30 patients (11 out of 15 PAR and 5 out of 15 NONPAR patients) suffered from mild residual neglect. Influence of neglect was calculated in an ANOVA using the between-subject factor Neglect (patient with neglect, without neglect), and the within-subject factors Target Position (target at previous target location, at previous distractor location, at

previously empty location) and Side (target in left, in right hemi-field). Level of significance was 5%.

ANOVA revealed all main effects (Neglect: [$F(1, 28) = 14.78$; $p < .01$], Target Position: [$F(2, 27) = 83.14$; $p < .01$], and Side [$F(1, 28 = 21.01$; $p < .01$], as well as the interactions Neglect × Target Position [$F(2, 27) = 5.78$; $p < .01$] and Neglect × Side [$F(1, 28) = 10.52$; $p < .01$] to be significant.

In both, patients without as well as patients with neglect RTs at previous target positions (without neglect: M = 803.43 ms, SD = 207.84; with neglect: 1125.45 ms, SD = 263.57) were significantly lower (without neglect: $t(13)$ -4. 97; $p < .01$; with neglect: $t(15) = -8.28$; $p < .01$) and significantly higher (without neglect: $t(13) – 4.11$; $p < .01$; with neglect: $t(15) = -5.23$; $p < .01$) at previous distractor positions (without neglect: M = 949.43 ms, SD = 236.98; with neglect: M = 1375.74 ms, SD = 338.83) compared to neutral positions (without neglect: M = 893.80 ms, SD = 62.64; with neglect: M = 1282.05 ms, SD = 318.50), indicating facilitation and inhibition in patients with and without neglect.

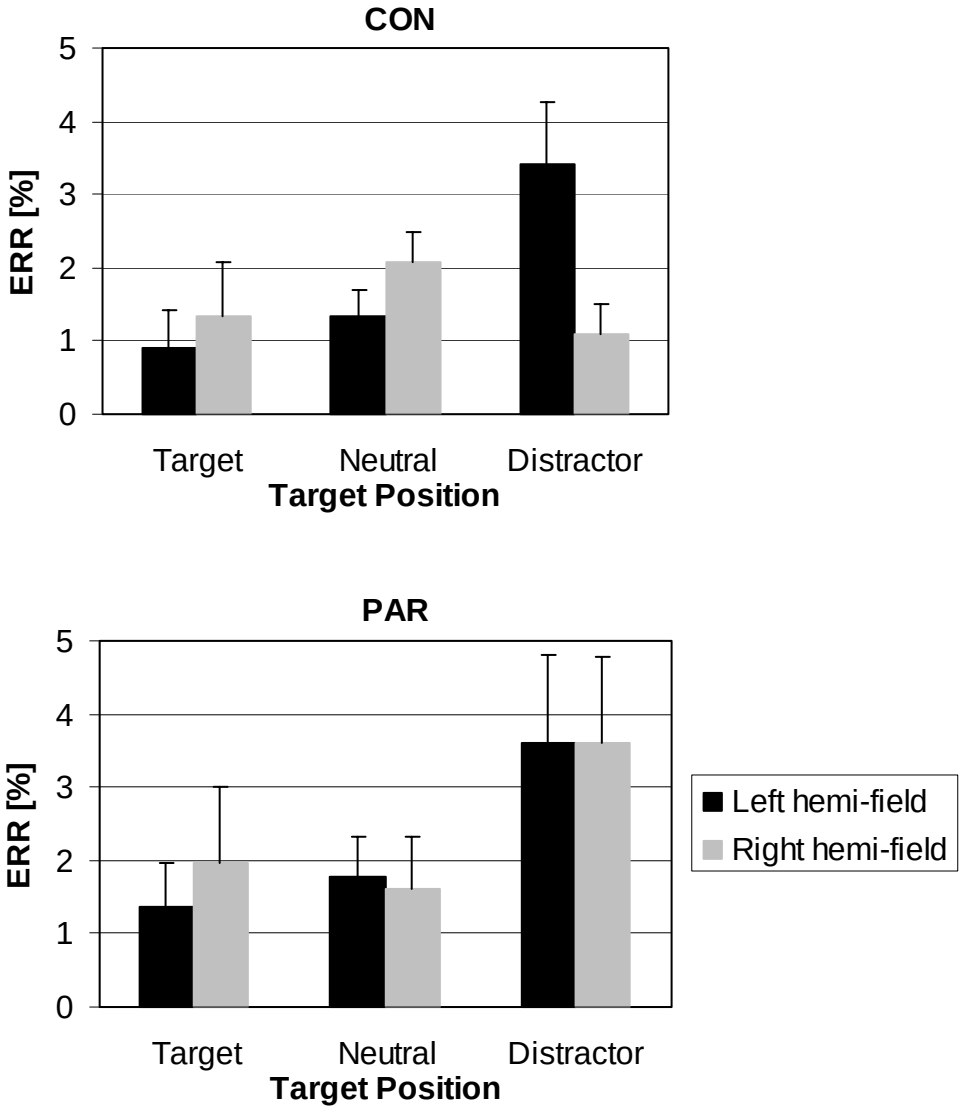
Comparing RTs of patients with and without neglect at the target positions, respectively, t-test revealed that compared to patients without neglect patients with neglect reacted significantly slower to targets at all target positions (previous target positions ($t(28) = -3.68$; $p < .01$; neutral positions ($t(28) = -3.75$; $p < .01$; previous distractor positions ($t(28) = -3.94$; $p > .01$).

In both patient groups, RTs to targets in the left were significantly higher compared to targets in the right hemi-field. However, this lateralisation effect was more pronounced in patients with neglect ($t(15) = 4.30$, $p < .01$) compared to patients without neglect ($t(13) = 2.79$; $p < .05$). The Target Position × Side and the Neglect × Target Position × Side interactions were non-significant (ps > .50).

Albeit the significant Neglect × Target Position ($p < .05$) interaction, further comparisons between patients with and without neglect indicated that relative facilitation ($p >$

.25) and inhibition ($p > .65$), respectively, were comparable in magnitude between patients with and without neglect.

Accuracy



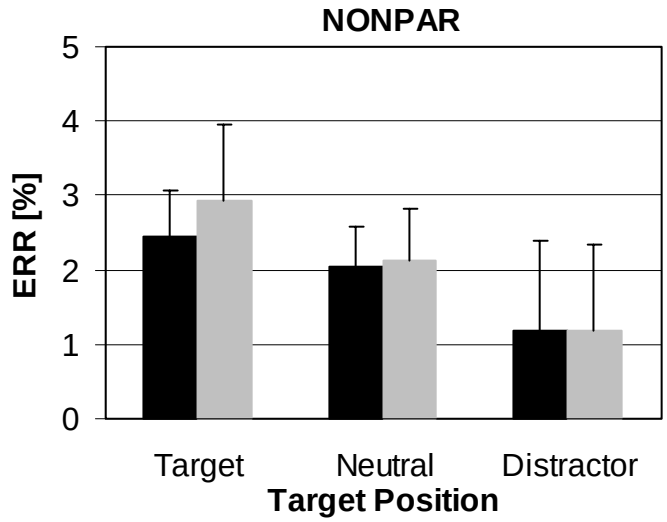


Figure 26. *Error percentage rates (ERR%) at the three target positions (target, neutral, and distractor) in the left and the right hemi-field for each group (CON, PAR, NONPAR) are depicted. Error bars indicate standard errors.*

Err% at the three target positions in the left and the right hemi-field for the patient and the control groups, respectively, are shown in figure 26.

The ANOVA revealed the interaction of Group × Target Positions to be highly significant [$F(4, 84) = 5.52$, $p < .01$]. PAR group were significantly more error prone ($t(14) = -2.38$; $p < .0.5$) for responses to targets at previous distractor ($M = 3.61$ %, $SD = 4.05$) compared to neutral positions ($M = 1.69$ %, $SD = 2.3$), indicating inhibition. Err% at the different target positions did not differ significantly in the CON ($p > .10$) and in the NONPAR group ($p > .05$).

All main effects (Group, Target Position, Side), and the interactions of Group × Side, Target Positions × Side, and Group × Target Position × Side were non-significant (all *p*s .10).

3. 3 Discussion

Previously presented visual information affects performance in current trials. A priming of pop-out paradigm was designed to measure experience from previous trials in current trials. By means of a specific distribution of RTs and errors at three different target

positions in terms of location-based facilitation and inhibition, the integrity of spatio-temporal integration of visual information across trials is signified (Maljkovic & Nakayama, 1996). In the present "control experiment" (7) we presented search arrays sequentially and without interference between subsequent trials.

Err% of the CON group reflected facilitation while they reflected inhibition in the PAR group. RTs revealed the characteristic pattern of facilitation and inhibition in all groups.

We replicated results of facilitation and inhibition in healthy subjects (Maljkovic & Nakayama, 1996; Geyer, Müller, & Krummenacher, 2007; see also "control experiment" (1) of study 1, II. chapter, p.28). Furthermore, we demonstrated that location priming is preserved in both hemi-fields in patients with right-hemispheric lesions with and without parietal involvement. Notwithstanding higher RTs in the left compared to the right hemi-field (which is in accordance with an approach of biased competition of visual attention; Desimone & Duncan, 1995; Peers, Ludwig, Rorden, Cusack, Bonfiglioli, et al., 2005), and in line with previous findings of patients with right-hemispheric lesions showing slowed RTs to left-sided targets ; e.g. Behrmann, Ebert, & Black, 2004). Preserved location priming in patients with right-hemispheric lesions is in line with previous results in studies which showed preserved facilitation (Kristjánsson et al., 2005) and facilitation and inhibition (Finke et al. in press) in patients with neglect after right-hemispheric lesions.

In the present study, relative facilitation was even enhanced in the PAR group as compared to the CON and the NONPAR group, while the magnitude of relative inhibition was comparable across all groups. This result does not suggest a deficit in spatio-temporal integration of successive visual information. Rather it brings out support in line with the notion that facilitation and inhibition might reflect different mechanisms that underlie visual search (Maljkovic & Nakayama, 1996), and hence are differentially susceptible by different factors (Geyer et al., 2007, Geyer and Müller, submitted). Recent results of location priming in right-hemispheric patients (Finke et al., in press) suggest that specific lesion sites might

have a specific impact on facilitation or inhibition, selectively. The current result suggests that lesions exhibited by PAR group patients increased facilitatory priming but did not alter inhibitory priming.

Basically, and crucial with regard to the aim of the present study, the presence of location priming effects signified the integrity of spatio-temporal integration of visual information across subsequent trials. The important implication of this result is that the current paradigm established with the “control experiment” (7) provides a useful method to investigate effects on location priming induced by interfering events between sequential trials. Thus, it is suitable for the aim of the study to investigate possible, and determine specific, circumstances which might hinder integration of visual information across space and time. Deficient integration would be reflected by disturbed location priming effects.

In the “saccade experiment” (8) the influence of saccades on location priming was studied. The fixation cross was presented in turns on the left and on the right side of the monitor. Subjects had to conduct a saccade accordingly. The search array was presented around the fixation cross (consistently with the “control experiment”). Hence priming was measured in retiotopically equal coordinates after the saccade, providing post-saccadic circumstances that did not require spatial remapping to re-locate activity foci on the saliency map. Crucially, the experiment allowed for measuring the pure influence of saccades on location priming without the influence of spatial remapping.

4. SACCADE EXPERIMENT (8)

4. 1 Method

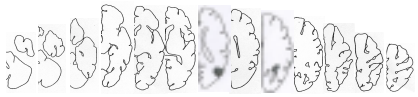
4. 1. 1 Participants

Selection criteria and procedure match the "control experiment" (7). Patients were again assigned to two groups according to their lesion site (see figure 27). 11 PAR patients and 12 NONPAR patients took part in the saccade experiment. Patients were tested at a median of 11 and within a range of 1 up to 57 weeks post injury. The patient groups did not differ significantly with respect to time since brain injury [$F(1, 21) = 1.34$; $p > .25$].

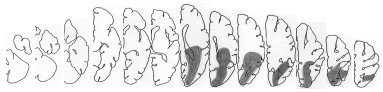
PAR:

DR 

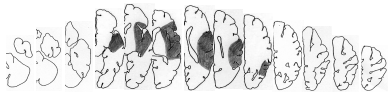
ML 

KL 

RL 

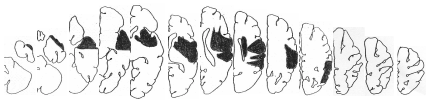
KF 

SW 

MP 

HG 

SH 

JM 

KS 

NONPAR:

TH 

EG 

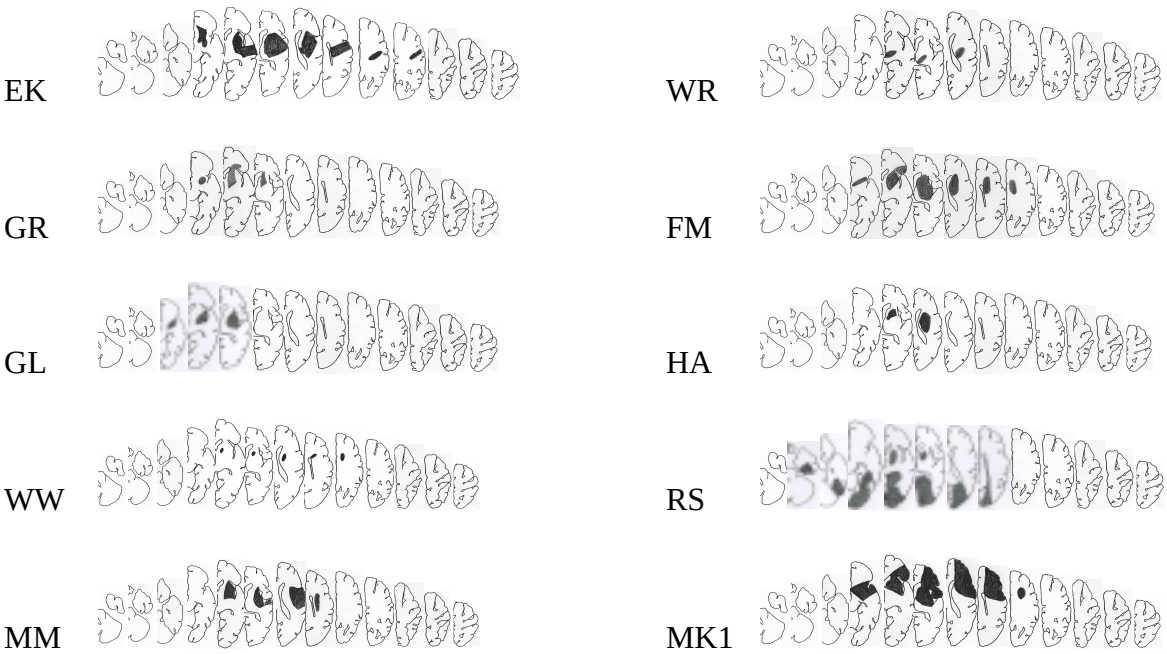
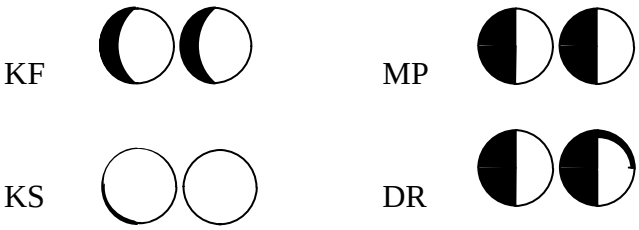


Figure 27. *Lesion reconstructions of the 23 patients*

The patient data were compared to the data of 11 age- and education matched control subjects (CON). Patient groups did not differ significantly from the CON groups with respect to age [$F(2, 31) = .45$, $p > .60$] or education [$F(2, 31) = 0.38$, $p > .65$]. Demographical information is given in table 2. Patients with field defects as assessed in the clinical standard diagnosis are depicted in figure 28. Two patients (one of the PAR, one of the NONPAR group) were left-handed.

PAR:



NONPAR:

RS 

Figure 28. *Visual field defects of patients with (PAR) and without (NONPAR) parietal lobe lesions are depicted.*

Table 2

Group demographics and clinical information. Gender distribution, median and range for age, education, and time since injury, residual neglect

	sex (f/m)	age [years]	education [years]	TSI [weeks]	Injury type (CVA/Tu)	Residual neglect
CON	5/6	56 (34–71)	10 (8–13)	-	-	-
PAR	4/7	49 (27–78)	10 (8–13)	13 (1–57)	11/0	7
NONPAR	0/12	64 (34–79)	10 (8–13)	11 (3–28)	10/1	4

4. 1. 2 Materials

Stimuli were the same as in the “retinotopic experiment” (2) in study 1, II. chapter, p. 34.

Note that in the current experiment a given target stimulus could appear at the following locations (s. figure 29): in trials following a saccade from the right to the left fixation cross: either on the left side (left hemi-field) or on the right side (right hemi-field) of the search array around the fixation cross on the left side of the monitor; in trials following a saccade from the left to the right fixation cross: either on the left (left hemi-field) or on the right side (right hemi-field) of the search array around the fixation cross on the right side of the monitor. Analogously to the control experiment (7) “Side” refers to either the left or the

right side within a search array, relative to the fixation cross, and, thus, to the visual hemi-field of the subject.

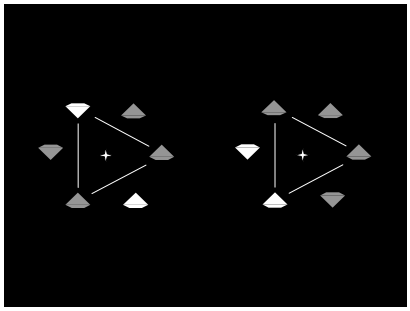


Figure 29. *Six stimuli positions around a fixation cross in the left or the right half of the monitor screen, respectively, were possible. The three stimuli (one target, two distractors) appeared either around the fixation cross in the left half or the right half of the screen, with the presentation side switching from trial to trial.*

4. 1. 3 Procedure

Procedure was the same as in the "retinotopic experiment" in study 1, II. chapter, p.34.

RTs and errors were recorded for the left and right hemi-field, separately for targets appearing after saccades from the right to the left and from the left to the right fixation cross, respectively.

If necessary, break durations between experimental blocks were adjusted to patients´ individual requirements.

4. 2. Results

ANOVAs with the same factors as in the "control experiment" (7) were conducted. RTs at the three target positions for the left and the right hemi-field for all groups are depicted in figure 30.

Reaction times

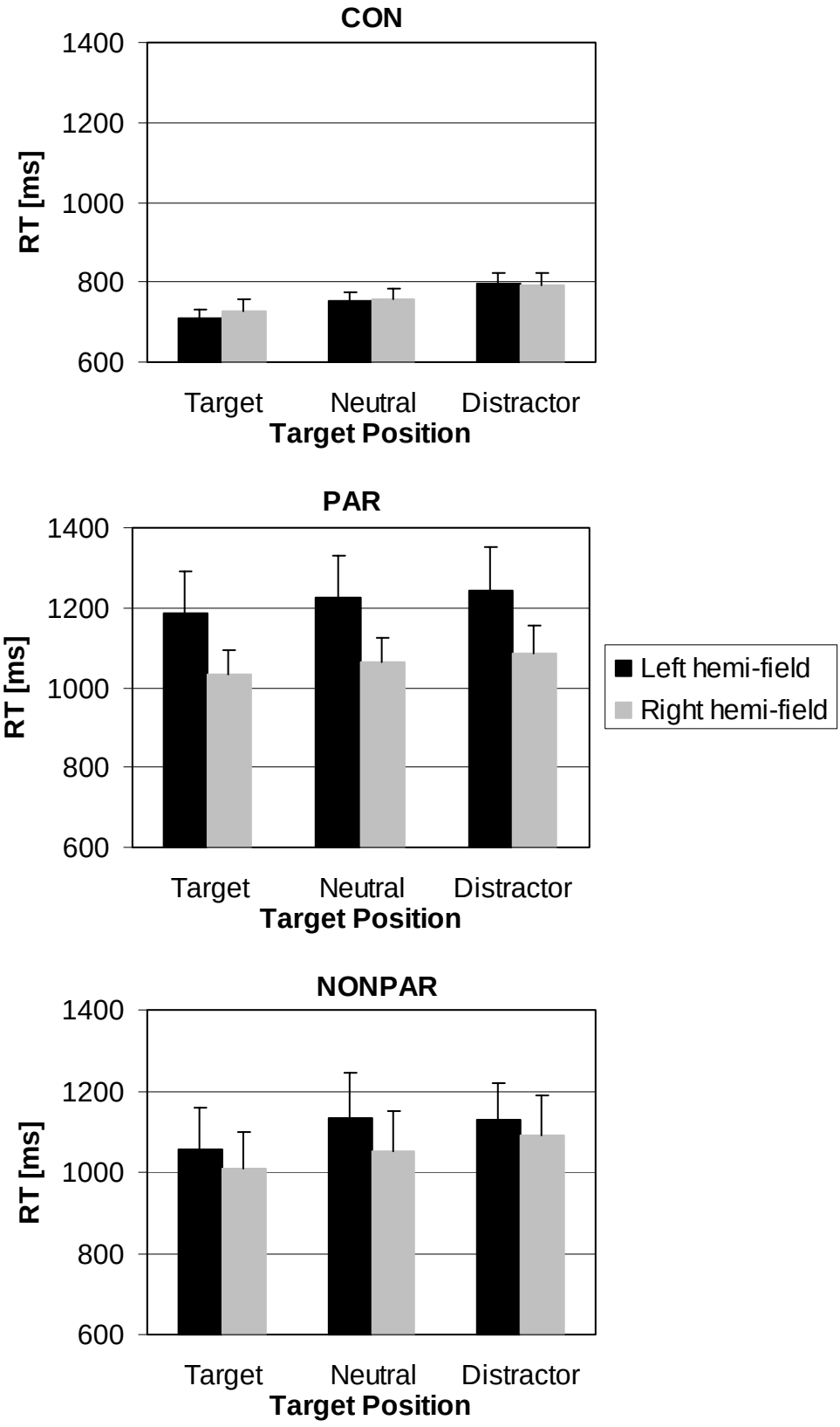


Figure 30. *Mean reaction times (RT) at the three target positions (target, neutral, and distractor) in the left and the right hemi-field for each group (CON, PAR, NONPAR), respectively are depicted. Error bars indicate standard errors.*

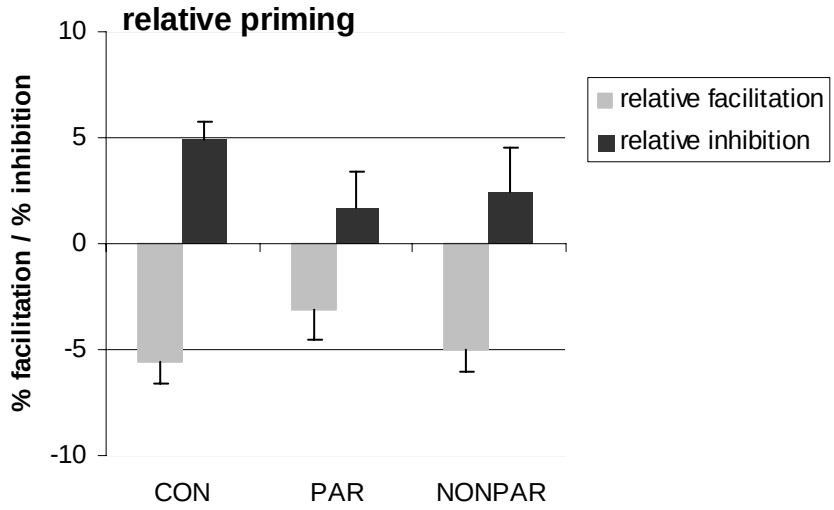


Figure 31. *Relative priming effects (facilitation and inhibition in percent) is depicted for each group (CON, PAR, NONPR), separately. Error bars indicate standard errors.*

The ANOVA revealed all main effects (Group: [$F(2, 31) = 7.\ 98$, $p < .01$], Target Position [$F(2, 30) = 19.68$, $p < .01$]), and Side [$F(1, 31) = 10.32$; $p < .01$], as well as the interaction Group × Side [$F(2, 31) = 4.83$; $p < .05$] to be significant.

Across all groups, RTs at previous target positions (M = 957.70 ms, SD = 289.26) were significantly lower ($t(33) = -5.58$; $p < .01$) and significantly higher ($t(33) = -2.13$; $p < .05$) at previous distractor positions (M = 1026.74 ms, SD = 289.01) compared to neutral positions (M = 1002.01 ms, SD = 300.99) indicating facilitation and inhibition across all groups.

In the PAR and NONPAR group RTs on targets in the left were significantly higher (PAR-R group: $t(10) = 2.55$; $p = .05$), NONPAR group: $t(11) = 2.84$; $p < .05$) compared to targets in the right hemi-field. In the CON group, RTs to targets in the left were comparable to the right hemi-field ($p > .55$).

The interactions of Group × Target Position, Target Position × Side, and Group × Target Position × Side were non-significant (all ps > .55).

Accuracy

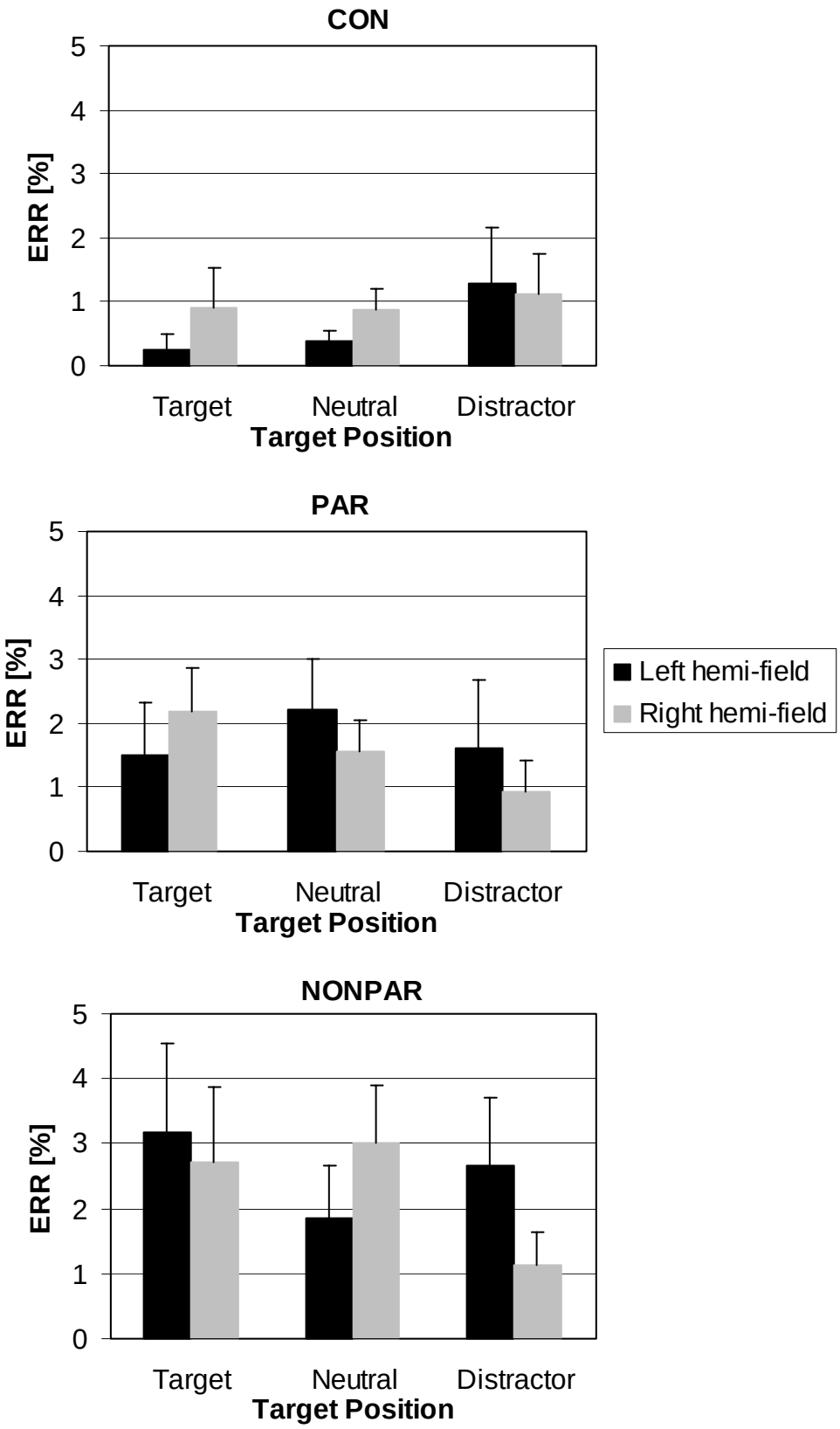


Figure 32. *Error percentage rates (ERR%) at the three target positions (target, neutral, and distractor) in the left and the right hemi-field for each group (CON, PAR, NONPAR) are depicted. Error bars indicate standard errors.*

Err% at the three target positions in the left and the right hemi-field for each group are shown in figure 32. The ANOVA revealed a tendency for a significant Target Position × Side interaction (p = .90). All main effects (Group, Target Position, Side) and further interactions (Group × Target Position, Group × Side, and Group × Target Position × Side) were non-significant (all ps > .15).

4. 3 Discussion

In previous studies spatial remapping was required along with and concurrently induced by saccades (e. g. Husain et al., 2001; Shimozaki et al., 2003). Some used goal-directed saccades themselves to draw conclusions upon remapping mechanisms (s. double-step saccade task, e.g. Heide et al., 1995). These procedures implicate unavoidably that impacts on the respective tasks due to saccades themselves, such as motor problems of conducting saccades or problems with planning saccades, are confounded with impacts of spatial remapping necessary to compensate for saccades.

The “saccade experiment” (8) provided a method to disentangle demands of saccadic eye movements from that of spatial remapping. Subjects had to conduct saccades between sequentially presented trials but nevertheless the stimuli were presented at retinotopically equal locations after the saccades. Hence, in terms of the model by Pisella and Mattingley (2004), activities on locations of the saliency map were not re-located. Accordingly, facilitatory and inhibitory location priming, reflected by RTs, was present and consistent across all groups. This result is congruent with expectations based on the finding in study 1, II. chapter, p.22 and the study by Sapir et al. (2004) who showed transfer of IOR into retinotopical coordinates in healthy subjects and patients with right parietal lesions, respectively.

Saccadic eye movement per se, i.e. without spatial remapping requirements did not disturb spatio-temporal integration of visual information in the PAR group as indicated by the

presence of location priming effects in this group. Effects were comparable to effects in the CON and the NONPAR group. Saccades were used to implement spatial remapping requirements in the “spatial remapping experiment” (9). In that sense the “saccade experiment” (8) functions as an additional control experiment for the “spatial remapping experiment” (9).The fixation cross was presented in turns on the left and on the right side while the search array was presented constantly in the centre of the monitor. Subjects had to conduct saccades between subsequent trials comparable to the requirements of the “saccade experiment” (8). However, they viewed the centrally presented search array in turns from the left and from the right side of fixation. A successful integration of visual information required compensation for the saccadic displacement of the search array by spatial remapping in-between sequential trials.

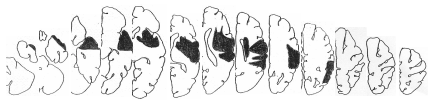
5. SPATIAL REMAPPING EXPERIMENT (9)

5. 1 Method

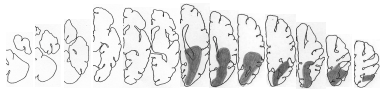
5. 1. 1 Participants

Selection criteria and procedure match the previous experiments. Patients were again assigned to two groups according to their lesion sites (see figure 33). 9 PAR patients and 7 NONPAR patients[3] were included in the analyses of the "spatial remapping experiment" (9). Patients were tested at a median of 14 and within a range of 1 up to 57 weeks post injury. The patient groups did not differ significantly with respect to time since brain injury [$F(1, 14) = 0.51$; $p > .45$].

PAR:

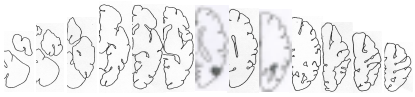
JM 

SW 

KF 

DR 

HG 

KL 

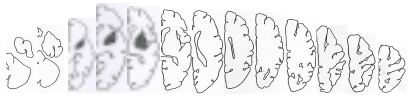
SH 

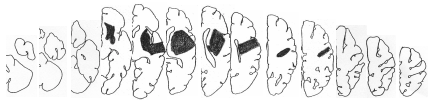
ML 

KS 

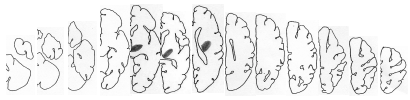
[3] 1 patient with a lesion to the basal ganglia had to be excluded due to extremely high RTs, presumably caused by an alertness deficit often caused by lesions to the basal ganglia (Chow & Cummings, 1999).

NONPAR.

GL 

EK 

TH 

WR 

RS 

WW 

EG 

Figure 33. *Lesion reconstructions of the 16 patients*

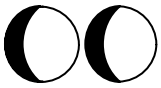
The patient data were compared to the data of 9 age- and education matched control subjects (CON). Patient groups did not differ significantly from the CON groups with respect to age [$F(2, 22) = .21$, $p > .80$] or education [$F(2, 22) = 0.08$, $p > .90$]. Demographical information is given in table 3. Patients with field defects are depicted in figure 34. One patient of the PAR group was left-handed.

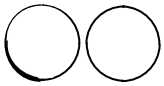
Table 3

Group demographics and clinical information. Gender distribution, median and range for age, education, and time since injury, residual neglect

	sex (f/m)	age [years]	education [years]	TSI [weeks]	Injury type (CVA/Tu)	Residual neglect
CON	6/3	57 (29 - 71)	10 (8 - 13)	-	-	-
PAR	4/5	51 (27 - 78)	10 (8 - 13)	9 (1 – 57)	9/0	5
NONPAR	0/7	65 (34 - 82)	10 (8 - 13)	11 (4 –20)	6/1	2

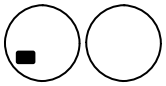
PAR

KF 

KS 

DR 

NONPAR

WR 

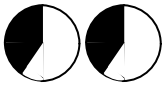
RS 

Figure 34. *Visual field defects of patients with (PAR) and without (NONPAR) parietal lobe lesions are depicted.*

5. 1. 2 Materials

The experimental set-up equalled the "spatiotopic experiment" (3) in study 1, II. chapter, p. 37, in the present thesis.

5. 1. 3 Procedure

Task and procedure equalled the "spatiotopic experiment (3) in study 1, II. chapter, p. 37.

Reaction times and errors were recorded separately for targets viewed from the left and targets viewed from the right side of the screen (or respectively: after saccades from the right to the left and after saccades from the left to the right side).

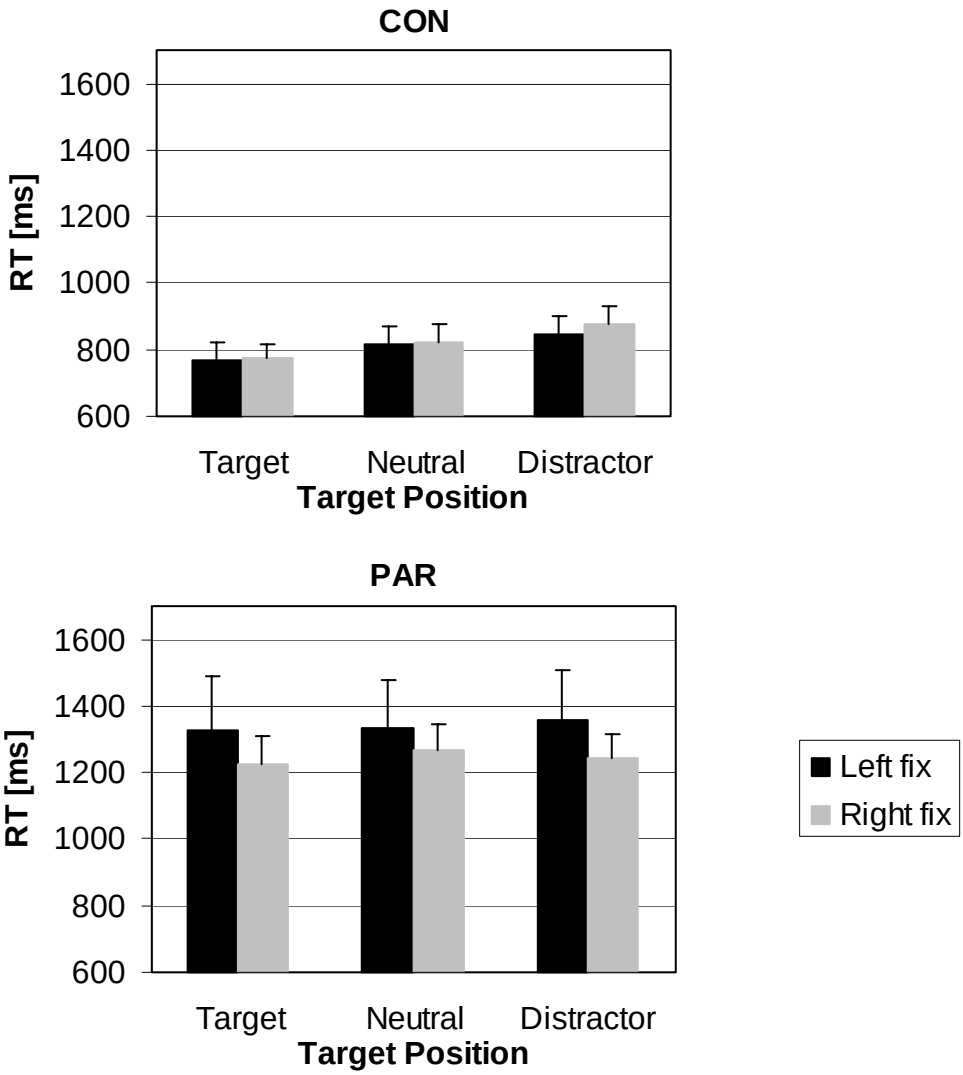
If necessary, break durations between experimental blocks were adjusted to patients´ individual requirements.

5. 2 Results

The dependent variables RTs (excluding error trials and trials following an error trial, as well as extreme values 2 standard deviations above or beneath mean RTs of the respective

target position) and accuracy (err%) were examined in separate ANOVAs using the same factors as in the ANOVAs conducted for the previous experiments with one exception. The search array was presented centrally while spatial remapping requirements between subsequent trials were implemented by eye movements from a peripherally left towards a peripherally rightwards and vice versa presented fixation cross. Thus, the within-subject factor Side (s. "control" and "saccade experiment") was replaced by the factor Fixation cross (left; right).

Reaction times



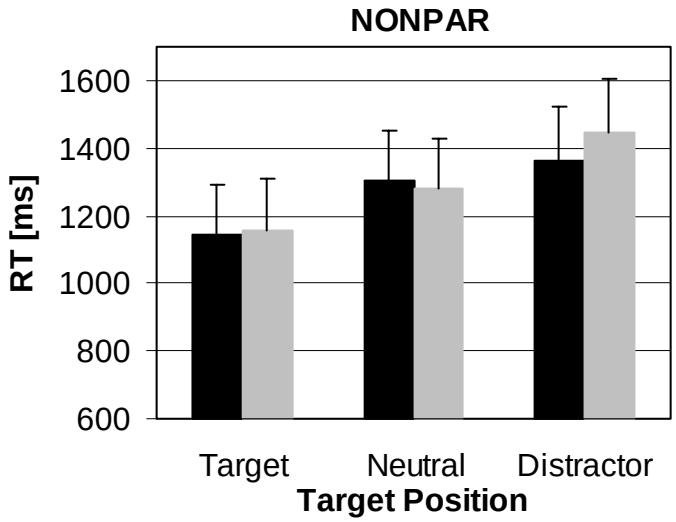


Figure 35. *Mean reaction times (RT) at the three target positions (target, neutral, distractor) are depicted, separately for trials presenting the fixation cross on the left(Left fix) and on the right side (right fix) of the monitor screen, respectively. Error bars indicate standard errors.*

For each group mean RTs at the three target positions, separately for trials presenting the fixation cross on the left and on the right side of the monitor screen, respectively are shown in figure 35.

The ANOVA of the RTs revealed the main effects of Group [$F(2, 22) = 6.99$; $p < .01$], Target Position [$F(2, 21) = 26.13$; $p < .01$] as well as the Group × Target Position interaction [$F(4, 44) = 7.39$, $p < .01$].

In the CON and NONPAR group, RTs at previous target positions were significantly lower (CON group: $t(8) = -5.44$; $p < .01$; NONPAR group: $t(6) – 7.86$; $p < .01$) and significantly higher (CON group: $t(8) = -3.52$; $p < .01$; NONPAR group: $t(6) = -3.57$; $p < .05$) at previous distractor positions compared to the neutral conditions, indicating facilitation and inhibition. However, in the PAR group RTs at previous target ($p > .45$) and distractor positions ($p > .95$) were comparable to neutral positions, indicating that neither facilitation nor inhibition was preserved in the PAR group. Relative priming effects (in percent) are depicted in figure 36.

The main effect of Fixation cross, as well as the two- and the three way interactions were non-significant (all *p*s > .10).

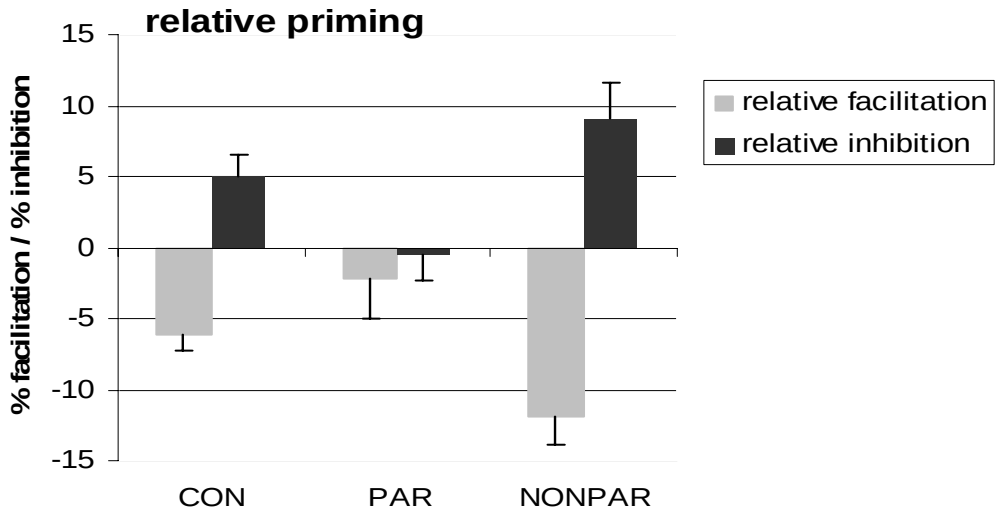


Figure 36. *Relative priming effects (facilitation and inhibition in percent) are depicted for the three groups. Error bars indicate standard errors.*

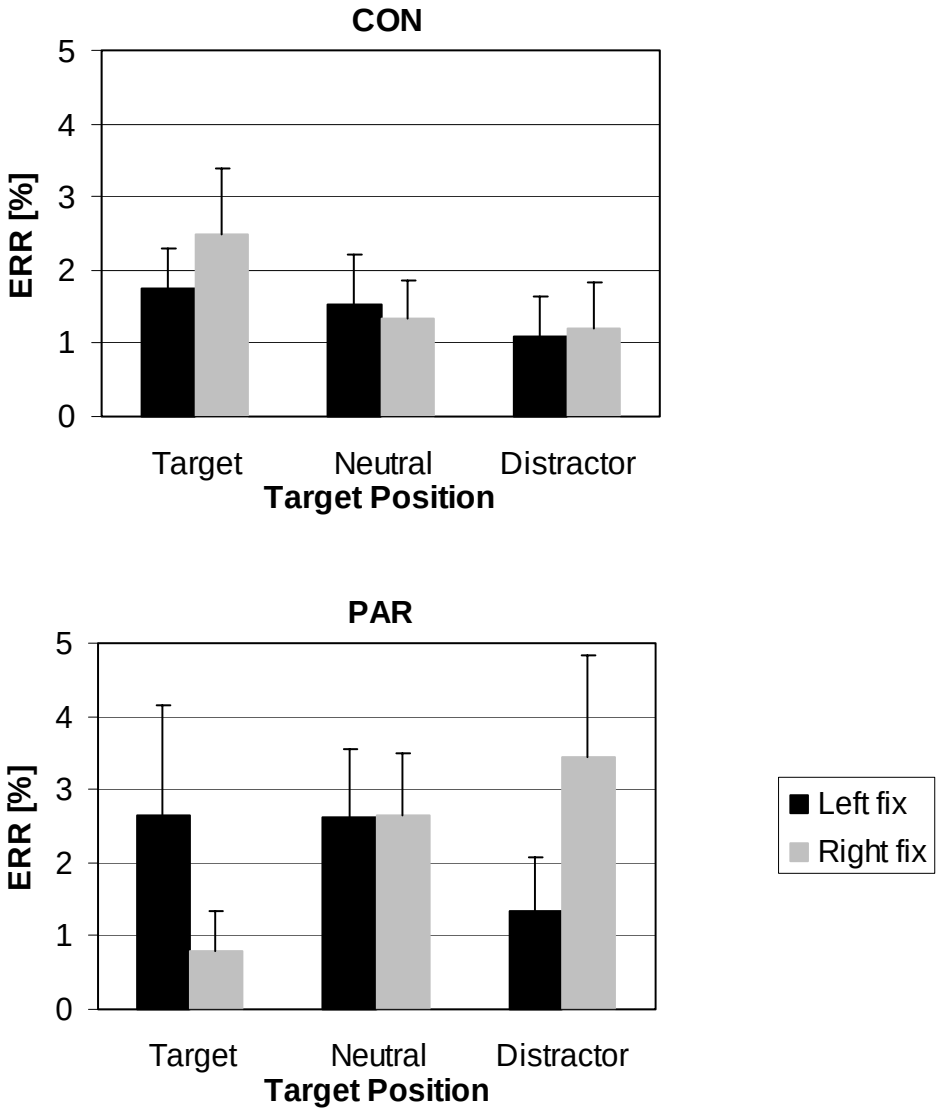
Influence of neglect

Since there was a significant Group × Target Position interaction factors which might have influenced priming effects were examined closer. 7 out of 16 patients (5 out of 9 PAR and 2 out of 7 NONPAR patients) suffered from mild residual neglect. The influence of neglect was calculated analogously to the "control experiment" (7), with the implied difference that the former within-subject factor Side was exchanged by the factor Fixation cross. Level of significance was 5%. Below-stated results focus on the influence of neglect. Previously reported results are not repeatedly remarked in detail.

The main effects of Neglect [$F(1, 14) = 8.23$; $p < .05$] and Target Position [$F(2, 13) = 6.87$; $p < .01$] were significant. RTs of patients with neglect (M = 1519.10 ms, sd = 384.55) were significantly higher ($t(14) = -2.87$; $p < .05$) compared to RTs of patients without neglect (M = 1157.10, sd = 176.48).

The main effect of Side and the two- and the tree-way interactions (including those with the factor Neglect) were non-significant (all *p*s > .35).

Accuracy



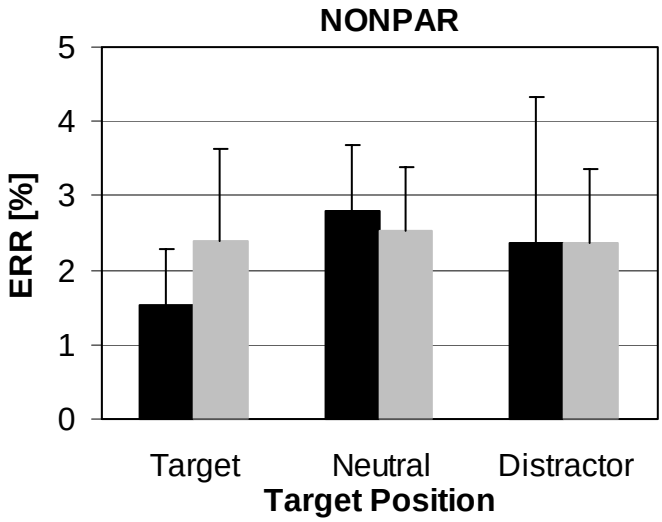


Figure 37. *Error percentage rates (ERR%) at the three target positions (target, neutral, distractor) in trials presenting the fixation cross on the left (Left fix) and on the right side of the monitor screen (Right fix) are depicted for each group (CON, PAR, NONPAR), respectively. Error bars indicate standard errors*

.

Err% for each group are shown at the three target positions for trials presenting the fixation cross on the left and on the right side of the monitor screen, respectively in figure 37. The ANOVA revealed all main effects and possible interactions to be non-significant (all *p*s > .15).

5. 3 Discussion

In the "spatial remapping experiment" (9), as revealed by the RTs, subjects of the CON and NONPAR group showed intact facilitatory and inhibitory priming, while PAR patients did neither show facilitation nor inhibition. The non-significant accuracy data did not suggest any alternative interpretation of the RTs results.

The results demonstrate the ability of healthy subjects and patients with right-hemispheric lesions without parietal involvement to establish a spatio-temporal consistency by integrating visual information despite spatial remapping requirements. The result obtained in the CON group replicates the result obtained in the "spatiotopic experiment" (3) in study 1, II. chapter, p.37, in the present thesis. The result obtained in the NONPAR group is in

accordance with our expectations that patients with lesions not involving the parietal lobe demonstrate intact spatio-temporal integration processes due to intact spatial remapping mechanisms.

Priming was not preserved in the PAR group. Patients of this group showed neither facilitation nor inhibition. The lack of priming indicates that visual information had not been integrated across space and time after remapping requirements. In accordance with the model proposed by Pisella and Mattingley (2004) data of the present study suggest spatial remapping deficits after right parietal lesions.

6. Conclusion

In three different priming of pop-out experiments we tested the integrity of integration of visual information across space and time in healthy subjects and in patients with unilateral right-hemispheric brain lesions with and without parietal involvement. Successful integration of previously provided visual information based on intact spatial remapping (Pisella & Mattingley, 2004) was indicated by the presence of location-based facilitatory and inhibitory priming (Chun & Nakayama, 2000).

The most crucial finding was a complete lack of priming in the PAR group in the "spatial remapping experiment" (9). In this experiment saccades which were required between the trials caused a spatial displacement of the search array in ego-centric coordinates. Consequently, spatial remapping was required to compensate for the displacement. In terms of the model suggested by Pisella and Mattingley (2004) activity foci on the saliency map have to be re-located after saccades by spatial remapping. Information represented on the saliency map is important to accomplish this re-positioning. However, the model predicts that right parietal lesions lead to an overwriting of the information on the saliency map along with saccades (contra-lateral information loss after right-ward saccades and complete loss after left-ward saccades). Our results are in line with the model's prediction. In terms of the model,

in the “spatial remapping experiment” (9) saccades which were conducted from the left to the right or the right to the left side of the screen, after each trial, led to a complete loss of information represented on the saliency map in PAR patients. Accordingly, these patients failed to integrate previously presented visual information across subsequent trials. The failure of integration is reflected by the absence of both, facilitatory and inhibitory location priming effects. In contrast, healthy subjects as well as NONPAR patients showed facilitation and inhibition, and thus signified intact integration presumably based on intact spatial remapping mechanisms.

In the “control experiment” (7) without interfering events such as saccades or spatial remapping requirements, all groups showed significant facilitation and inhibition. The effect of facilitation was even enhanced in the PAR group as compared to the NONPAR and the CON group. Note that albeit this result suggests a specific influence on facilitation but not inhibition in the PAR group, it does not derogate the outcome of preserved priming which is crucial here. The presence of priming effects in all groups indicates that visual information had been successfully integrated across subsequently presented trials in a condition without interfering events (such as saccades or spatial remapping requirements) between subsequent trials.

In the “saccade experiment” (8) a saccade had to be conducted between subsequent trials but nevertheless the search array was presented in retinal equal coordinates, thus – in terms of the model by Pisella and Mattingley (2004) – activity foci on the saliency map were not needed to be re-positioned by spatial remapping after saccades. This method allowed for disentangling the influence of saccades from the influence of spatial remapping on priming effects. Both, facilitatory and inhibitory priming effects were found to be present across all groups, indicating the integrity of spatio-temporal contingency.

As suggested by Pisella and Mattingley (2004), spatial remapping deficits in patients with parietal lesions might account for characteristic impairments in visual search. The

present result of deficient spatial remapping mechanisms in patients with right parietal lesions, points directly at the crucial role of spatial remapping abilities in visual search since these patients demonstrate impairments in spatio-temporal integration of visual information in a visual search task. Given distinguishable roles for location-based facilitatory and inhibitory priming underlying visual search behaviour (Geyer et al., 2007, Finke et al., in press; Geyer & Müller, submitted) conclusions on visual deficits might be drawn accordingly. A lack of facilitation might contribute to explain the random search pattern following an inability to integrate visual information provided by preview displays as found by Shimozaki et al., (2003). Shimozaki et al. (2003) presented a preview display with stimuli at certain locations. In a subsequently presented display, the target stimulus for which subjects had to look for was presented. Thereupon, the search display which was identical with the preview display was presented. Patients with right parietal lesions showed random search patterns while looking for the target item in the search display. In contrast to healthy subjects who conducted a goal-directed saccade towards the target stimulus, patients were apparently not able to benefit from the visual information provided by the preview display. In terms of the model by Pisella and Mattingley (2004) and contrasted against the background of results in the present study, we might suggest that visual information which was provided by the preview display had been overwritten on the saliency map in patients with right parietal lesions along with the interference provided by the display which presented the target stimulus. Accordingly, patients had to start anew (without preview information) when looking for the target stimulus in the search display.

Inhibition of targets at previous distractor positions had been suggested to be similar in function to IOR (Maljkovic & Nakayama, 1996), i.e. to inhibit orienting to irrelevant (inhibition at previous distractor positions) or previously examined locations (IOR; Klein & MacInnes, 1999), respectively. Hence, a lack of inhibition in terms of the inability to tag

irrelevant or previously searched locations might contribute to explain a phenomenon such as revisiting behaviour (Husain et al., 2001; Pisella et al, 2004; Malhotra et al., 2005).

IV. CHAPTER

STUDY 3

DO COVERT SHIFTS OF ATTENTION INDUCE SPATIAL REMAPPING REQUIREMENTS? EVIDENCE FROM PATIENTS WITH RIGHT PARIETAL LESIONS

1. Abstract

In order to provide a reliable representation of the external world by integration of visual information across space and time a model by Pisella and Mattingley (2004) assumes spatial remapping mechanisms to constantly update information on a saliency map (Niebur & Koch, 1989). Spatial remapping is required along with changes on the saliency map due to spatial shifts of attention, which can occur overtly, accompanied by saccades and covertly, without saccades. Based upon evidence that the parietal lobe is crucially involved in spatial remapping (Duhamel et al., 1992b; Merriam et al., 2003) and that patients with parietal lesions exhibit spatial remapping deficits after saccadic shifts of attention (e.g. Heide et al., 1995) the model assumes the parietal cortex to provide the neural substrate for the saliency map. Further support is also provided by the results of study 2, III. chapter, p.56, in the present thesis.

The current study was designed to obtain evidence from patients with parietal lesions whether covert shifts of attention would induce spatial remapping requirements as assumed by the model. To that end we analysed the integrity of spatio-temporal integration of visual information by means of location-based priming in a priming of pop-out paradigm. In three experiments we analysed facilitatory and inhibitory priming effects in a group of healthy subjects (CON) and patients with right-hemispheric lesions with (PAR) and without parietal involvement (NONPAR). In the “control experiment” (10) no attention shifts were induced in-between subsequent trials. In the “nonrelevant distractor” (11) and “relevant distractor experiment” (12) covert attention shifts were induced by peripheral distractors, exogenously and endogenously, respectively. Provided that spatial remapping takes place in the parietal cortex after covert attention shifts we expected disturbed priming in the PAR group in the “nonrelevant distractor” (11) and “relevant distractor experiment” (12).

However, facilitation and inhibition was present across all groups and experiments, indicating intact spatio-temporal integration. We contrast the finding against the background of the model.

2. Introduction

To provide a seamlessly continuing and coherent spatial representation of our dynamic environment, the representation needs to be updated along with changes in the environment, and self-movements (Medendorp et al., 2002; Rushworth & Taylor, 2006). To avoid "snapshot" perception along with the overwriting of information (Tatler, 2001) visual input provided by each single eye fixation needs to be integrated across space and time. This integration process has been suggested to be accomplished by spatial remapping (Colbyet al., 1995; Pisella & Mattingley, 2004; Gottlieb, 2007). However, very little is known about the exact mechanisms of spatial remapping (Morris et al., 2007). A model proposed by Pisella and Mattingley (2004) assumes spatial remapping mechanisms to operate on a saliency map (Itti & Koch, 2001), before salient information on the map is subsequently selected for conscious representation by spatial attention (Niebur & Koch, 1998; Itti & Koch, 2001). After the most salient stimulus has been selected, activity on the saliency map at the selected location is suppressed and attention is re-allocated to the location of the next-highest salient stimulus on the saliency map and so on (Itti 2000). A stable construct of the environment evolves from constant (re-) allocation of overt and covert attention to locations of salient stimuli on the map.

Based upon its important role for space representation (Colby & Goldberg, 1999) and spatial remapping (Duhamel et al.,1992a; Farrell & Robertson, 2000) the model by Pisella and Mattingley (2004) proposes the parietal cortex as neural substrate for the saliency map. Accordingly, deficient spatial remapping mechanisms which follow parietal lesions hinder the integration of visual information across space and time, and thus the establishing of stable

spatial arrays. The model assumes spatial remapping requirements after shifts of attention. Attention in order to enhance processing at a new location can be shifted in two ways. Firstly, overtly, i.e. accompanied by saccadic eye movements, and secondly, covertly, without co-occurring eye movements. However, it is not clear whether covert shifts of attention provide spatial remapping requirements the way overt shifts of attention do as assumed by the model.

Results in patients provide evidence for remapping after overt shifts (Duhamel et al., 1992b; Heide et al., 1995). In the "spatial remapping experiment" (9) in study 2, III. chapter, p. 88, we showed that spatial remapping requirements are induced by saccadic, i.e. overt shifts of attention. In accordance with the model's assumption, lesions to the parietal cortex had been shown to disturb spatio-temporal integration of visual information when saccadic remapping was required. Given a tight linkage of overt and covert attention it is likely that covert attention shifts induce spatial remapping requirements similarly the way saccades do.

As suggested by the "premotor theory of attention" (Rizolatti, Riggio, Dascola, & Umiltá, 1987) saccadic preparation involves the same process as shifting attention, and vice versa saccades are associated with attentional shifts. This is supported by behavioural findings which demonstrate that covert attention precedes saccadic eye movements (Deubel & Schneider, 1996) and vastly by evidence from functional neuroanatomy of visual attention and saccadic eye movements. Both activate similar underlying fronto-parietal networks (Fink, Dolan, Halligan, Marshall, & Frith, 1997, Corbetta et al., 1998; Nobre et al., 2000; Beauchamp et al., 2001), including the lateral intraparietal area (LIP; Goldberg, Bisley, Powell, & Gottlieb, 2006), and moreover structures known to specifically play a role in saccade preparation such as the superior colliculus (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004). Reciprocally, microsaccades along with covert shifts of attention had been found to subliminally activate the oculomotor system (Hafed & Clark, 2002).

However, there is evidence that overt and covert attention shifts can occur separately. Posner, Cohen, & Rafal (1982) demonstrated intact covert shifts of attention in a patient with

progressive supranuclear palsy who was on the contrary unable to conduct saccades. Recently, Khan, Blangero, Rossetti, Salemme, Luauté et al. (in press) demonstrated dissociation between the ability to conduct saccades accurately and to shift attention covertly in a patient with posterior parietal damage. Results from patient studies hence suggest that the co-activation of common neural networks by overt and covert attention shifts might rather reflect functional coupling than inevitable linkage of the two ways of attentional shifting.

Moreover, covert shifts of attention were shown to have different impacts on visual perception as well as on neurophysiological mechanisms compared to overt attentional shifts. Object-invariant recognition (Cox et al., 2005) and form adaptation (Melcher, 2007) was found to be modifiable by overt but not by covert shifts of attention. Furthermore, in the study by Duhamel et al. (1992b) 44 % of the studied LIP neurons in monkeys have been shown to compensate for saccadic eye movements, i.e. overt shifts of attention by exhibiting anticipatory (or predictive) remapping of upcoming target locations. Most of the LIP neurons (96 %) showed memory-based remapping i.e. they discharged when a saccade brought the site of a flashed stimulus into the neuron's receptive field, even though the stimulus itself was no longer present. The cell firing occurred in response to a visual memory trace which had been remapped in conjunction with the eye movement. Critically, LIP neurons did not remap in response to covert shifts of attention, i.e. neither predictive nor memory-based remapping occurred in the absence of saccadic eye movements (Duhamel et al. 1992b). Since the parietal cortex had been found to be essentially involved in spatial remapping presumably based on the characteristic behaviour of LIP neurons (Heide et al., 2001; Merriam et al., 2003; Bellebaum, Hoffman, & Daum, 2005; Heiser et al., 2005; Berman et al., 2007; Morris et al., 2007) it is not clear whether spatial remapping requirements are induced by covert shifts of spatial attention per se.

There are findings, which support the assumption of spatial remapping after covert shifts of attention. Vasquez and Danckert (2008) recently found direction-specific (higher in

the right than in the left hemi-field) decrements on the performance in a spatial working memory task after overt and (even higher costs) after covert shifts of attention. The authors argue that the decrement on spatial working memory performance emanates from “memory-based remapping” (s. definition below). However, these results were obtained in a paradigm involving a spatial displacement of the search array along with the covert attention shift, and thus do not provide evidence for the assumption made by Pisella and Mattingley (2004, p. 187) that covert attention shifts entail spatial remapping in the course of which activity foci on the saliency map are re-freshed rather than re-located.

The current study used a paradigm that allows for disentangling spatial displacement of the spatial search array from covert shifts of attention, thus investigate the pure impact of covert attention. The study was designed to obtain evidence from patients with parietal lesions - since the parietal cortex was proposed as the anatomical correlate for spatial remapping after overt and covert attention shifts (Pisella & Mattingley, 200) - whether covert shifts of attention would induce spatial remapping requirements the way overt shifts of attention do. To that end, we applied a priming of pop-out paradigm (Maljkovic & Nakayama, 1996) which had been successfully established before as a method to investigate spatial remapping mechanisms (study 2, III. chapter, 56).

In a priming of pop-out paradigm the integrity of spatio-temporal integration of subsequently presented information – as supposed to be accomplished by spatial remapping mechanisms – is indicated by location priming effects (Chun & Nakayama, 2000). Facilitatory and inhibitory priming reflect previous experience from the preceding trial, and thus can be measured as a function of the preceding trial: Targets appearing at previous target locations are detected faster and more accurately (facilitation), while detection of targets at previous distractor locations is slower and more error-prone (inhibition). We analysed location priming effects in three different experiments. In each experiment, two groups of right-hemispheric lesioned patients, with (PAR) and without parietal involvement

(NONPAR), and a group of age- and education matched subjects (CON) participated, respectively.

In the “control experiment” (10) no shifts of attention between subsequent trials were required. We expected to replicate findings of facilitation and inhibition in healthy subjects (Maljkovic & Nakayama, 1996; Geyer et al., 2007) in the CON group. As previously shown, location priming in visual pop-out search without interfering events and unlimited presentation time of search displays similar to the task used in the “control experiment” (10) is preserved in neglect patients (Kristjánsson et al., 2005). Complementary, Finke et al. (in press) found both, facilitatory and inhibitory priming in right hemispheric patients with neglect. Albeit, Finke et al. (in press) provided evidence that facilitation and inhibition might reflect two different underlying mechanisms in visual search (Maljkovic & Nakayama, 1996; Geyer et al.. 2007) by demonstrating that inhibitory but not facilitatory priming was selectively affected in two patients with lesions to the frontal eye fields priming was basically preserved in these patients. Hence, we expect priming to be present in the “control experiment” (10), in PAR and NONPAR patients.

In experiment 11 and 12 covert attention shifts were induced in-between subsequent trials. Distractor stimuli were flashed randomly on the left or the right side of the screen. There is evidence that covert attention shifts occur by support of two distinct mechanisms, reflexive orienting towards exogenously and voluntary orienting towards endogenously triggering stimuli (Müller & Rabbitt, 1989). We investigated covert attention shifts after both. The “irrelevant distractor” (11) and the “relevant distractor experiment” (12) provided conditions of covert attention shifts by exogenous and endogenous orienting, respectively. In the “irrelevant distractor experiment” (11) the peripheral distractors were task-irrelevant and thus triggered covert attention shifts exogenously. In the “relevant distractor experiment” (12) a secondary task was conjoint with the peripheral distractors, thus covert attention was shifted voluntarily (endogenously).

Based on previous findings in the “nonrelevant distractor” (5) and “relevant distractor experiment (6) in study 1, II. chapter, 22, priming effects were expected to be present in the CON group. Furthermore, they were expected to be preserved in NONPAR patients given that their lesions spared the parietal lobe. Based on previous findings in the “spatial remapping experiment” (9) in study 2, III. chapter, p.88, we expected priming effects to be altered or disturbed in the PAR group provided that covert attention shifts (exogenously and / or endogenously) actually induce spatial remapping requirements. Conversely, preserved priming (after exogenous and / or endogenous covert attention shifts) in the PAR group would suggest that the respective covert attention shifts do not induce spatial remapping in the way overt attention shifts do.

3. CONTROL EXPERIMENT (10)

3. 1 Method

3. 1. 1 Participants

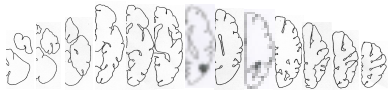
Patients with right sided brain damage were recruited from a neurological rehabilitation clinic. They were assigned to either of two groups, on the basis of their injury location, with parietal involvement (PAR) or without parietal involvement (NONPAR) as documented by the reports of previous radiological examinations. The assignment was confirmed by a second validation of CT/MR scans at the point in time of testing (see figure 38). 10 PAR patients and 8 NONPAR patients took part in the "control experiment" (10). All gave written informed consent to participate in the study, according to the declaration of Helsinki II. Patients were tested at a median of 10 and within a range of 1 up to 150[4] weeks post injury. The patient groups did not differ significantly with respect to time since brain injury [$F(1, 16) = .22$; $p > .60$].

PAR:

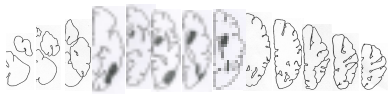
KF 

ML 

KS 

KL 

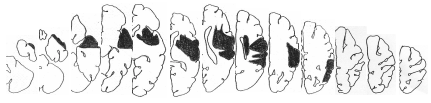
SW 

KW 

WK 

HG 

SH 

JM 

[4] Patients WK and HS suffer from old lesions. They were former patients of the rehabilitation clinic.

NONPAR:

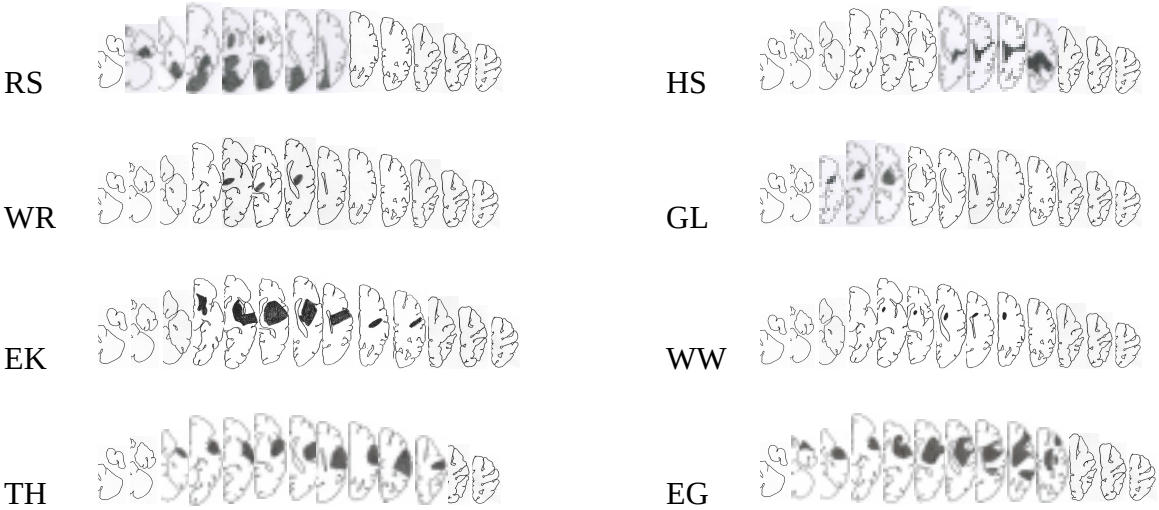


Figure 38. *Lesion reconstructions of the 18 patients. Lesions have been drawn onto standard slices from the Damasio template system (Damasio & Damasio, 1989). Only the affected right hemisphere is depicted.*
Abbreviations: PAR, group of patients with right-sided injury with parietal involvement; NONPAR, group of patients with right-sided injury without parietal involvement.

Patients with insufficient comprehension of instruction were excluded, as were patients with acute visual neglect, interfering with the perceptual requirements for the experimental task. Some of the patients with and without parietal lesions who participated in this study had have neglect after lesion onset. Although recovered in large part until the time of testing the patients might have suffered from residual mild neglect. Hence, the contingent contribution of neglect on the performance pattern was surveyed closely. Information about the presence of residual neglect symptoms are derived from standard diagnosis in the clinic.

The patient data were compared to the data of 10 age- and education matched control subjects (CON), who had no history of psychiatric or neurological disorder. Patient groups did not differ significantly from the CON group with respect to age [$F(2, 25) = .79$, $p > .45$] or education [$F(2, 25) = 1.15$, $p > .30$]. Demographical information is given in table 4.

Table 4

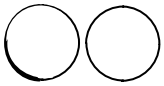
Group demographics and clinical information. Gender distribution, median and range for age, education, and time since injury, residual neglect

	sex (f/m)	Age [years]	education [years]	TSI [weeks]	Injury type (CVA/Tu)	Residual neglect
CON	5/5	58 (26 – 66)	11 (9 – 13)	-	-	-
PAR	4/6	49 (27 – 78)	10 (8 – 13)	7 (1 – 105)	10/0	5
NONPAR	1/7	66 (34 – 82)	10 (8 – 13)	12 (4 – 150)	7/1	2

Abbreviations: CON, healthy age and education matched control group

All patients and control subjects had either normal or corrected-to-normal visual acuity. Two patients of the PAR group and one patient of the NONPAR group suffered from partial visual field loss as assessed by clinical standard diagnostic. Visual field defects are depicted in figure 39. As assessed by a handedness-inventory, two patients (one of the PAR and one of the NONPAR group) and one control subject were left-handed.

PAR:

KF  KS 

NONPAR:

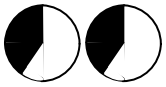
RS 

Figure 39. *Visual field defects of patients with (PAR) and without (NONPAR) parietal lobe lesions are depicted.*

3. 1. 2 Materials

Stimuli were the same as in the “long-ISI-control experiment” (4) in study 1, II. chapter, p. 41.

Note that no stimuli occurred on the imaginary vertical midline, permitting RTs and errors to be determined separately for the left and the right visual field (figure 40).

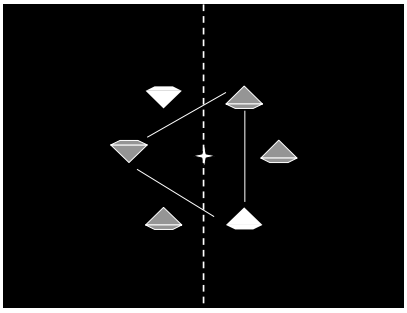


Figure 40. *Illustration of the search displays used in the "control experiment" (10). The red target (depicted as white diamond) appeared in either the left or right visual hemi-field together with two green distractors (depicted as gray diamonds). One possible search display is indicated by the connecting lines between the stimuli, another display is shown without connecting lines. No stimuli appeared on the imaginary vertical midline (illustrated by the dashed line).*

3. 1. 3 Procedure

The procedure was the same as in the "Long-ISI-control experiment (4) in study 1, II. chapter, p.41, RTs and errors were recorded for the left and right hemi-field, separately. If necessary, break durations between experimental blocks were adjusted to patients´ individual requirements.

3. 2 Results

The dependent variables RTs (excluding error trials and trials following an error trial as well as extreme values 2 standard deviations above or beneath mean RTs of the respective target position) and accuracy (err%) were examined in separate ANOVAs with the between-subject factors Group (CON, PAR, NONPAR), Target Position (target at previous target location, at previous distractor location, at previously empty location) and Side (target in left, in right hemi-field),. Level of significance was 5%.

Reaction times

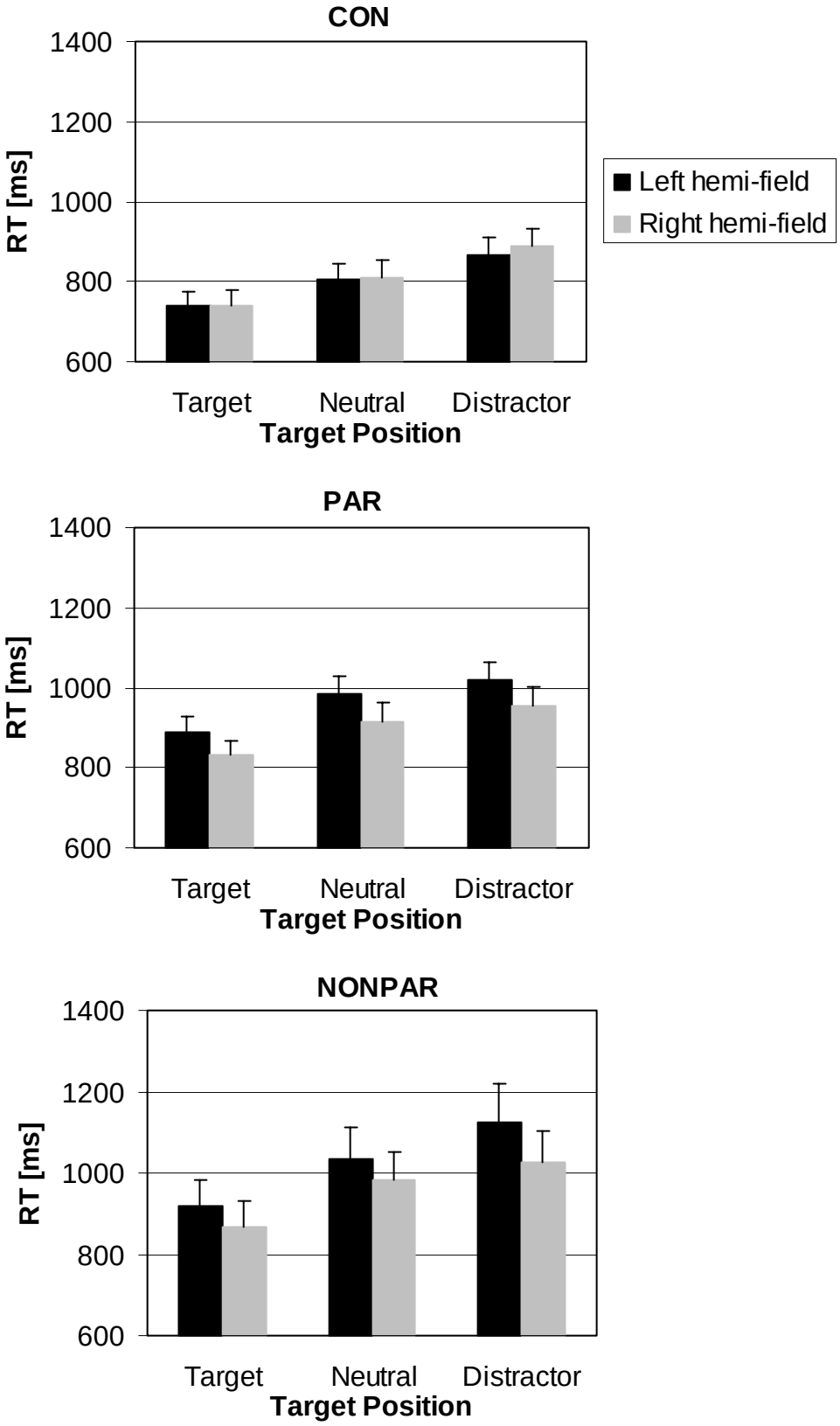


Figure 41. *Mean Reaction times (RT) at the three target positions (target, neutral, distractor) in the left and the right hemi-field are depicted for each group (CON, PAR, NONPAR), respectively.*

Mean RTs at the three target positions in the left and the right hemi-field of each group are shown in figure 41.

The ANOVA of the RTs revealed all main effects, (Group: [$F(2, 25) = 6.25$, $p < .01$], Target Position: [$F(2, 24) = 114.58$, $p < .01$], and Side: [$F(1, 25) = 7.41$, $p < .01$]), as well as the Group × Target Position interaction [$F(4, 50) = 4.39$; $p < .05$] to be significant. In all groups, RTs at previous target positions were significantly lower (CON: t (9) = -4.04; $p < .01$; PAR: t (9) = -4.5; $p < .01$; NONPAR: $t(7) = 5.83$; $p < .01$) and significantly higher (CON: $t(9) = -7.56$; $p < .01$; PAR: $t(9) = -3.41$; $p < .01$; NONPAR: $t(7) = -4.06$, $p < .01$) at previous distractor positions compared to neutral positions, indicating facilitation and inhibition in the CON, PAR, and NONPAR group, respectively.

RTs at previous target positions of the CON group were marginally significant lower ($t(18) = -2.10$; $p < .06$) compared to PAR, and significantly lower ($t(16) = -2.79$; $p < .05$) compared to NONPAR group. RTs at previous target positions of the PAR group were marginally significant lower ($t(16) = -1.83$; $p < .09$) compared to the NONPAR group. RTs at neutral positions of the CON group were marginally significant lower ($t(18) = -2.06$; $p < .06$) compared to the PAR, and significantly lower compared to the NONPAR group ($t(16) = -3.02$; $p < .01$). RTs at neutral positions of the PAR group were marginally significant lower ($t(16) = -2.03$; $p < .06$) compared to the NONPAR group. RTs at previous target positions of the CON group were comparable ($p > .15$) to the PAR group, and significantly lower compared to the NONPAR group ($t(16) = -2.97$; $p < .01$). RTs at previous distractor positions of the PAR group were significantly lower ($t(16) = -2.32$; $p < .05$) compared to the NONPAR group.

RTs were significantly higher ($t(27) = 2.43$; $p < .05$) in the left (M = 970.13 ms, SD = 245.85) compared to the right hemi-field (M = 934.64 ms, SD = 240.48). However, the Group x Side interaction was marginally significant [$F(4, 50) = 3.29$; $p < .06$]. While the CON group showed comparable RTs in both hemi-fields ($p > .35$), the NONPAR group showed a

tendency towards significantly higher RTs ($t(7) = 2.03$; $p < .09$), and the PAR group showed significantly higher RTs ($t(9) = 2.28$; $p < .05$) in the left compared to the right hemi-field.

The interactions Target Position × Side and Group × Target Position × Side were non-significant ($p > .55$).

Despite the fact that each group exhibited significant facilitation and inhibition, there seemed to be a difference in the magnitude of priming effects, as indicated by the significant Group × Target Position interaction. To directly compare priming effects, we calculated the facilitation and inhibition effects relative to the overall RTs (in percent). Given that there was no significant Target Position × Side, facilitation and inhibition effects were calculated across both hemi-fields, respectively (see figure 42). One-way ANOVAs were used to test for differences of relative facilitation and relative inhibition in the three groups (CON, PAR, and NONPAR), respectively. While relative facilitation was comparable ($p > .20$) across all groups, the difference of relative inhibition between the groups was marginally significant [$F(2, 25) = 3.10$; $p < .07$]. Latter result occurred because relative inhibition of the PAR group was significantly lower compared to the CON group ($t(18) = 2.68$; $p < .05$), while relative inhibition was comparable between the CON and the NONPAR, and between the PAR and the NONPAR group (ps $> .20$).

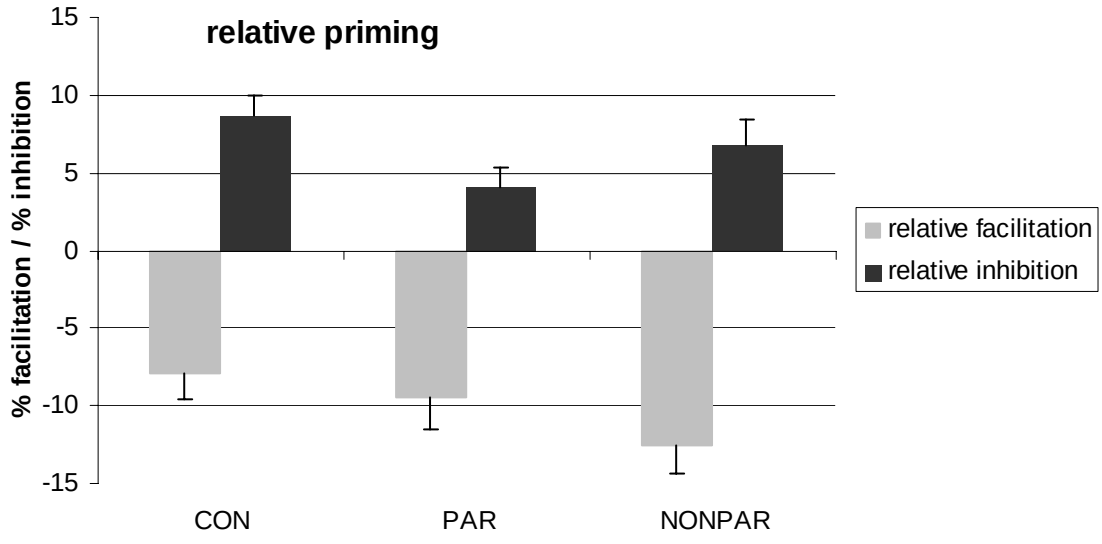


Figure 42. *Relative facilitation and inhibition in the three groups is depicted. Error bars indicate standard errors.*

Influence of neglect

To further investigate possible factors which might have influenced priming effects, we analysed the influence of neglect on priming effects. 7 out of 18 patients (5 out of 10 PAR and 2 out of 8 NONPAR patients) who participated in the "control experiment" (10) exhibited acute neglect after lesion onset. Influence of neglect was calculated in a separate ANOVA for the patient groups with the between-subject factor Neglect (patient with neglect, without neglect), and the within-subject factors Target Position (target at previous target location, at previous distractor location, at previously empty location) and Side (target in left, in right hemi-field). Below-stated results focus on the influence of neglect. Previously reported results are not repeatedly remarked in detail.

ANOVA revealed the main effects of Target Position [$F(2, 15) = 57.29$; $p < .01$] and Side [$F(1, 16 = 10.58$; $p < .01)$], to be significant. No influence of neglect was found, with the main effect Neglect, and further two-way and the three-way interaction (including the factor Neglect) non-significant (all *p*s > .10), indicating no influence of neglect.

Accuracy

Err% in all groups at all target positions in both hemi-fields are depicted in figure 43. All main effects (Group, Target Position, and Side) and interactions (Group × Target Position, Group × Side, Target Position × Side, and Group × Target Position × Side) were non-significant (all *p*s > .15).

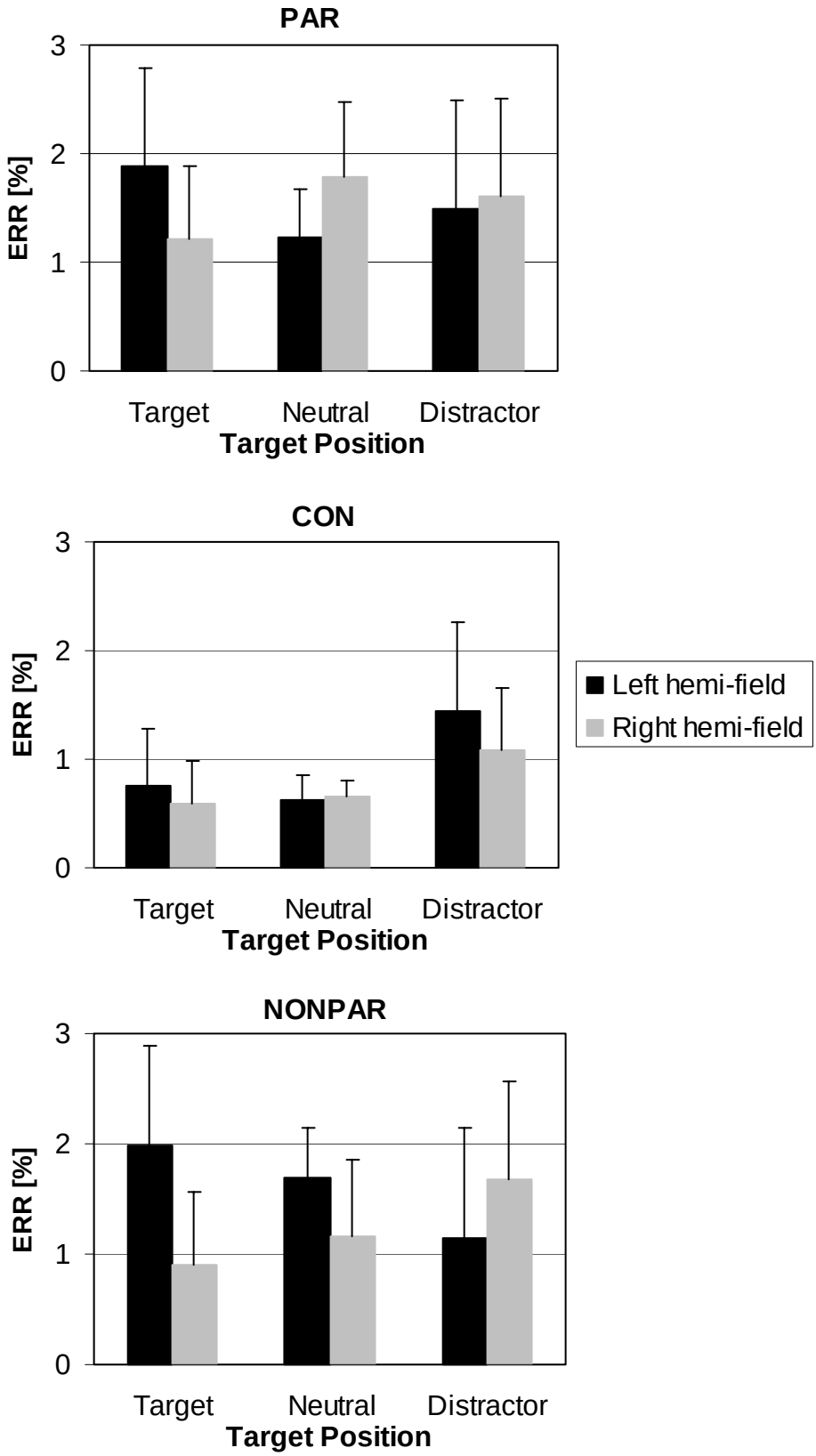


Figure 43. *Error percentage rates (ERR%) at the three target positions (target, neutral, distractor) on the left and the right side are depicted for each group (PAR-R, CON, NONPAR-R), respectively. Error bars indicate standard errors.*

3. 3 Discussion

Location-based priming of pop-out provides a method to measure integration of previously presented visual information across space and time. In particular, facilitatory and inhibitory priming is obtained at previous target and distractor positions (Maljkovic & Nakayama, 1996).This characteristic distribution of RTs and errors indicates the integrity of spatio-temporal contingency.

While accuracy did not differ at the different target positions across all groups, facilitation and inhibition was clearly reflected by RTs, and significantly present in all group.

Priming effects occurred in both hemi-fields, with the RTs comparable in the CON group, and the tendency for significantly higher RTs in the NONPAR group and significantly higher RTs in the left compared to the right hemi-field in the PAR group. The lateralisation of RTs in the patient groups is in accordance with an approach of biased competition of visual attention (Desimone & Duncan, 1995; Peers et al., 2005), and in line with previous findings of patients with right-hemispheric lesions showing slowed RTs to left-sided targets (e.g. Behrmann et al., 2004). Basically, the finding of priming effects in a pop-out paradigm without interfering events between subsequent trials replicates previous findings in healthy subjects (Maljkovic & Nakayama, 1996; Geyer et al., 2007), and in patients with right-hemispheric lesions (Kristjánnson et al., 2005; Finke et al., in press).

However, there was a significant Group × Target Position interaction which occurred because - despite significantly present facilitation and inhibition - relative inhibition in the PAR group was significantly reduced compared to the NONPAR and the CON group. Since successful spatio-temporal integration of visual information across subsequent trials in the PAR group is indicated by the presence of priming effects, the selective attenuation of inhibition but not of facilitation might have occurred in this group during the long ISI used in the present “control experiment” (10). More precisely, inhibition compared to facilitation has been found to be the less robust component (Geyer et al., 2007; Geyer & Müller, submitted)

and less endurable across time compared to facilitation (Maljkovic & Nakayama, 1996). In the present experiment, reduced inhibition in the PAR group (compared to the other groups) might hence reflect the impact of attention problems often associated with right parietal lesions (e.g. Pardo, Fox, & Raichle, 1991) on priming effects along with the long eventless ISI of 2,100 ms, rather than problems with integrating successive information.

Notwithstanding the fact of reduced inhibition in the PAR as compared to the NONPAR and CON group, both, facilitatory and inhibitory priming were significantly present in all groups. Importantly, regarding the aim of the present study, the presence of facilitation and inhibition basically suggests that integration of visual information across subsequent trials had successfully taken place. Thus, it is suitable for the aim of the study to investigate possible, and determine specific, circumstances which might hinder integration of visual information across space and time.

In the “spatial remapping experiment” (9), study 2, III. chapter, p. 88, in the present thesis, we showed that saccadic shifts of overt attention conducted in-between the trials, hindered integration of successive information in patients with right parietal lesions. The absence of both facilitatory and inhibitory priming was attributable to spatial remapping deficits in those patients.

Experiments 11 and 12 were designed to test whether covert attention shifts – provoked by peripheral distractors - between subsequent trials might also induce spatial remapping requirements. Evidence was taken from the performance of patients with right parietal lesions, since it had been shown that these patients do not show priming effects when spatial remapping is required in-between the trials.

Hence, provided that covert shifts of attention induce spatial remapping requirements similar to overt shifts of attention, we expect facilitatory and inhibitory priming to be affected after covert attention shifts between the trials in the PAR group.

By contrast, provided that covert attention shifts do not induce spatial remapping requirements, we would expect preserved priming effects after covert attention shifts in the PAR group. Moreover, in the latter case, and provided that reduced inhibition of the PAR group found in the “control experiment” (10) reflected consequences of attention deficits along with the long eventless ISIs, we would expect priming effects in the PAR group to be comparable to effects in the CON and the NONPAR group, given that peripheral distractors are flashed during the long ISIs in experiment 11 and 12, thus the ISIs are not longer eventless.

In order to induce covert shifts of attention, peripheral distractor stimuli were flashed in-between trials randomly on the left and the right side of the screen.

In the “irrelevant distractor experiment” (11) subjects were instructed to ignore the peripherally flashed distractors. However, it has been shown that reflexive orienting towards exogenously attention driving stimuli is automatic and not voluntarily suppressible (Jonides, 1981; Müller & Rabbitt, 1989). Hence, the peripheral distractors in the “irrelevant distractor experiment” (11) were supposed to activate reflexive orienting after each trial, although they did not have a task-related purpose such as e.g. predicting the spatial location of the target stimulus.

4. NONRELEVANT DISTRACTOR EXPERIMENT (11)

4. 1 Method

4. 1 1 Participants

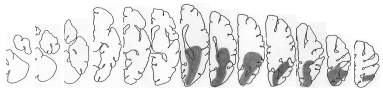
Selection criteria and procedure match the "control experiment" (10). Patients were again assigned to two groups according to lesion site (see figure 44). 10 PAR patients and 9 NONPAR patients took part in the "nonrelevant distractor experiment" (2). Patients were tested at a median of 10 and within a range of 1 up to 150[5] weeks post injury. The patient groups did not differ significantly with respect to time since brain injury [$F(1, 18) = .10$; $p > .75$].

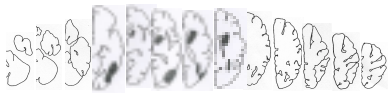
The patient data were again compared to the data of 10 age PAR:

SW 

ML 

JM 

KF 

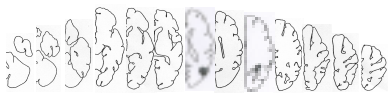
KW 

WK 

HG 

SH 

KS 

KL 

NONPAR:

[5] Patients WK and HS suffer from old lesions. They were former patients of the rehabilitation clinic.

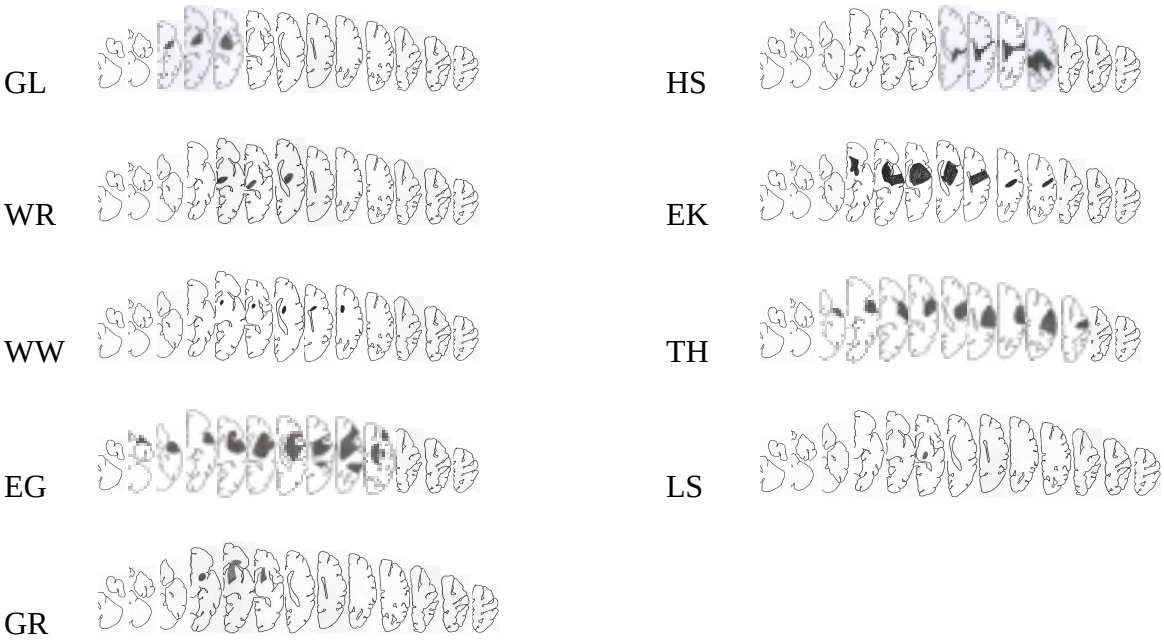


Figure 44. *Lesion reconstructions of the 19 patients.*

- and education matched control subjects (CON). Patient groups did not differ significantly from the CON groups with respect to age [$F(2, 27) = 1.15$, $p > .30$] or education [$F(2, 27) = 1.08$, $p > .35$]. Demographical information is given in table 5. Two patients of the PAR group suffered from partial visual field loss as assessed by clinical standard diagnostic. Visual field defects are depicted in figure 45. One patient of the PAR group was left-handed.

Table 5

Group demographics and clinical information. Gender distribution, median and range for age, education, and time since injury, residual neglect

	sex (f/m)	Age [years]	education [years]	TSI [weeks]	Injury type (CVA/Tu)	Residual neglect
CON	5/5	58 (26 – 66)	11 (9 – 13)	-	-	-
PAR	4/6	49 (27 – 78)	10 (8 – 13)	7 (1 – 105)	10/0	5
NONPAR	1/8	65.5 (34 – 82)	11.0 (8 – 13)	12 (3 – 150)	8/1	2

PAR:

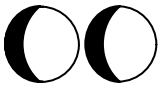
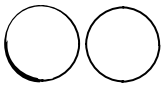
KF  KS 

Figure 45. *Visual field defects of 2 PAR patients are depicted*

4. 1. 2 Materials

Stimuli were the same as in the “irrelevant distractor experiment” (2) in study 2, III. chapter, p. 44.

4. 1. 3 Procedure

The procedure and task was the same as in the “irrrelevant distractor experiment” (2) in study 2, III. chapter, p.44. RTs and errors were recorded for the left and right hemi-field, separately. If necessary, break durations between experimental blocks were adjusted to patients´ individual requirements.

4. 2 Results.

ANOVAS including the same factors as in the control experiment (10) were conducted. Level of significance was 5%.

Reaction times

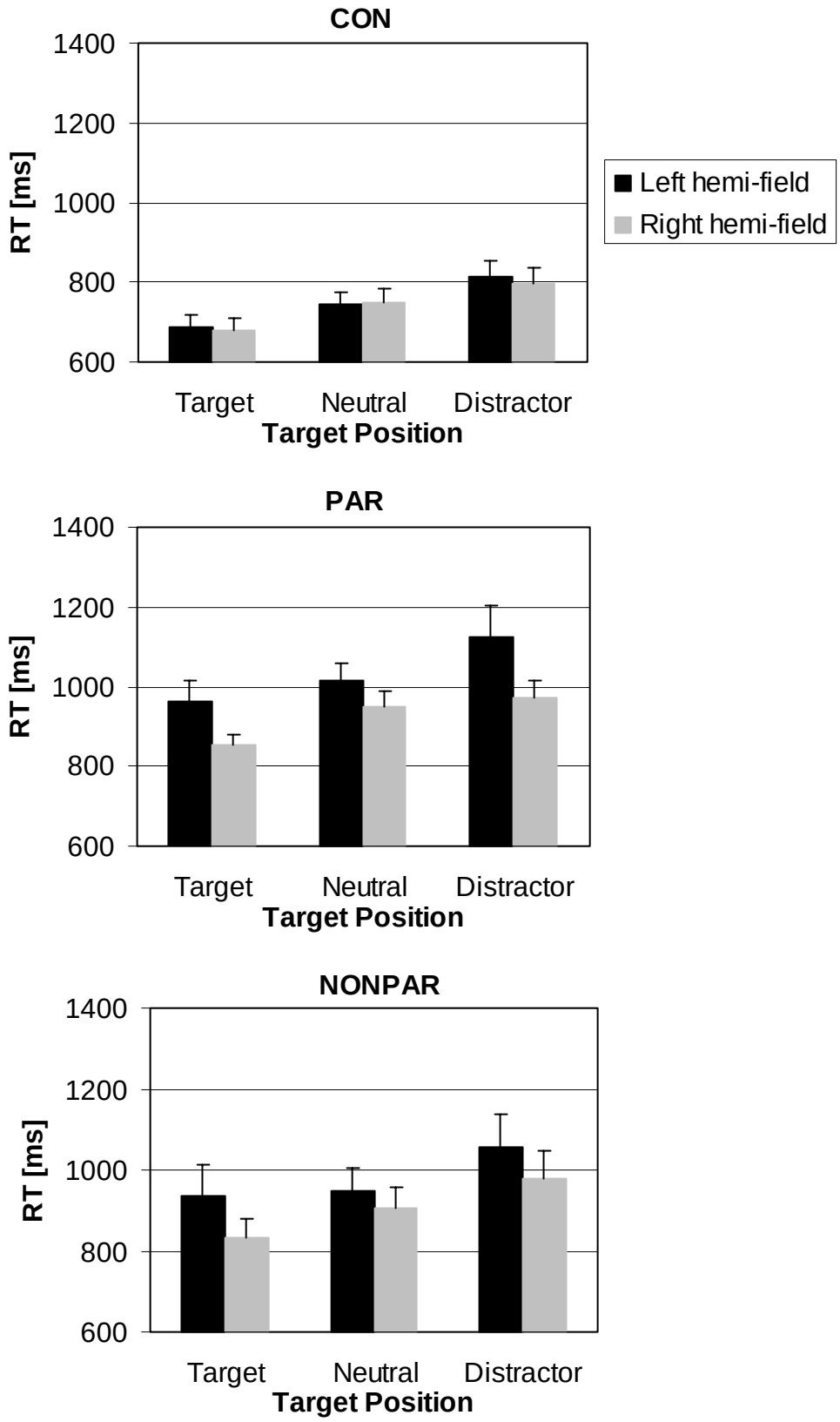


Figure 46. *Mean Reaction times (RT) at the three target positions (target, neutral, distractor) on the left and the right side are depicted for each group (CON, PAR, NONPAR), respectively. Error bars indicate standard errors.*

Mean RTs at the three target positions in the left and the right hemi-field, respectively for all groups, are shown separately in figure 46.

The ANOVA of the RTs revealed all main effects (Group: [$F(2, 26) = 5.36$, $p < .05$], Target Position: [$F(2, 25) = 47.43$, $p < .01$], and Side: [$F(1, 26) = 11.84$, $p < .01$]) as well as the Target Position × Side interaction [$F(2, 25) = 4.34$; $p < .05$] to be significant. The Group × Side interaction was marginally significant [$F(2, 26) = 2.76$; $p < .09$]. The interaction occurred because RTs in the left hemi-field were significantly higher compared to the right hemi-field in the patients groups (PAR: t (9) = 2.38; $p < .05$; NONPAR: t (8) = 3.13; $p < .05$) while they were comparable in both hemi-fields in the CON group ($p > .60$).

RTs of PAR and NONPAR group were significantly higher (t (17) = -2.74; p < .05) than RTs of the CON group. RTs of the PAR group did not differ significantly from RTs of the NONPAR group ($p > .30$).

RTs for targets at previous target positions in the left ($M = 917.10$ ms, $SD = 308.52$) and the right hemi-field ($M = 843.26$, $SD = 277.98$) were significantly lower (left hemi-field: $t(28) = -2.24$; $p < .05$; right hemi-field: $t(28) = -7.79$; $p < .01$) compared to neutral position in the left ($M = 952.87$ ms, $SD = 274.95$) and in the right hemi-field ($M = 923.79$ ms, $SD = 285.36$), respectively, indicating facilitation in both hemi-fields. RTs for targets at previous distractor positions in the left ($M = 1055.83$ ms, $SD = 274.95$) compared to neutral positions in the left hemi-field were highly significantly higher ($t(28) = -5.77$; $p < .01$, indicating inhibition in the left hemi-field. RTs at previous distractor positions in the right hemi-field did not differ significantly ($p > .15$) from RTs at neutral positions in the right hemi-field ($M = 923.79$ ms, $SD = 285.36$), indicating that there was no inhibition in the right hemi-field. Facilitation and inhibition effects relative to the overall RTs (in percent) in each hemi-field are depicted for each group, separately in figure 47.

RTs to targets at previous target and distractor positions in the left hemi-field were significantly higher (target: $t(28) = 3.18$; $p < .01$; distractor: $t(28) = 2.96$; $p < .01$) compared to

respective values in the right hemi-field. There was a tendency towards a significant difference between RTs at neutral positions in the left compared to respective values in the right hemi-field ($p < .08$).

The Group × Target Position and the Group × Target Position × Side interaction were non-significant ($ps > .50$).

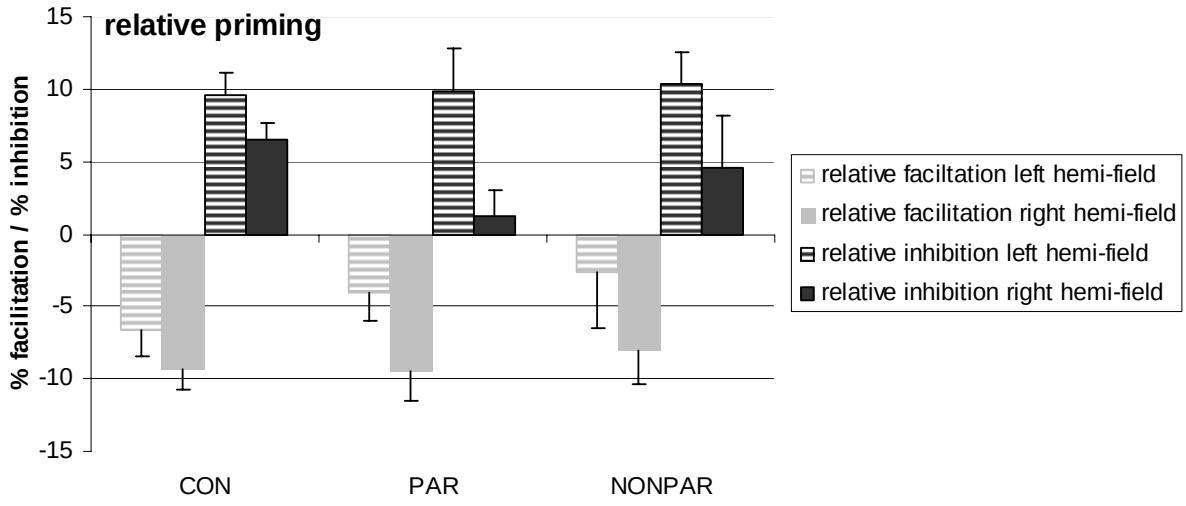


Figure 47. *Relative priming effects (facilitation and inhibition) in the left and right hemi-field for all groups are depicted. Error bars indicate standard errors.*

Influence of the presentation side of the peripheral distractor

Compared to the "control experiment" (10), a distinct pattern of RT data was found in the current experiment. Obviously, the peripheral distractors that triggered covert attention shifts exogenously had a certain lateralised influence on performance. Thus, we analysed whether the different sides of distractor presentation were differentially influencing priming effects.

Influence of the peripheral distractor in the left and the right hemi-field

The peripheral distractor could either appear in the left or in the right hemi-field, regardless of the side in which the target stimulus was presented. We analysed the influence of the presentation side of the peripheral distractor by calculating an ANOVA including the

same factors as above with the difference that the factor Side was replaced by the factor Distractor Side (distractor flashed in the left; in the right hemi-field).

ANOVA revealed the main effects Group [$F(2, 26) = 5.79$; $p < .01$] and Target Position [$F(2, 25) = 28.87$; $p < .01$] to be significant (s. further results reported above). The factor of Distractor Side was marginally significant [$F(1, 26) = 2.31$; $p < .08$]), resulting from the very marginally tendency ($t(28) = 1.71$; $p = 1.00$) of lower RTs after presentation of the peripheral distractors on the right (M = 918.79 ms, SD = 274.58) as compared to the left side (M = 937.71 ms, SD = 286.37).

All interactions (Group × Target Position, Group × Distractor Side, Target Position × Distractor Side, and Group × Target Position × Distractor Side) were non-significant (all ps > .10).

Influence of the peripheral distractor in the ipsi- and the contra-lateral hemi-field

The peripheral distractors which were flashed before the search array was presented could appear either in the same (ipsi-lateral) or in the opposite hemi-field (contra-lateral) with respect to the target stimulus. We analysed the influence of the peripheral distractor according to its flash location in the ipsi- vs. contra-lateral hemi-field calculating an ANOVA with the same factors as above with the exception that the factor Distractor Side was replaced by the factor relative Distractor Side (distractor flashed in the ipsi, contra hemi-field with respect to the target stimulus).

The ANOVA revealed the main effects of Group [$F(2, 26) = 5.36$; $p < .05$] and Target Position [$F(2, 25) = 47.43$; $p < .01$] to be significant (s. further results reported above). The main effect of relative Distractor Side as well as all interactions (Group × Target Position, Group × relative Distractor Side, Target Position × relative Distractor Side, and Group × Target Position × relative Distractor Side) were non-significant (all ps > .30).

Influence of neglect

Furthermore the influence of neglect on priming was analysed. 7 out of 19 patients (5 out of 10 of the PAR and 2 out of 9 of the NONPAR group) who participated in the current experiment exhibited residual mild neglect. Contingent contribution of neglect was calculated in an ANOVA with the between-subject factor Neglect (patient with neglect, without neglect) and the within-subject factors Target Position and Side. Below-stated results focus on the influence of neglect. Previously reported results are not repeatedly remarked in detail.

ANOVA revealed the main factor of Neglect [$F(1, 17) = 4.56$; $p < .05$], Target Position [$F(2, 16) = 21.20$; $p < .01$], Side [$F(1, 17) = 16.46$; $p < .01$] and the Target Position × Side [$F(2, 16) = 5.17$; $p < .05$] interaction significant. There was a tendency towards a significant Neglect × Side interaction ($p < .09$).

RTs of patients with neglect (M = 1207.23 ms; SD = 393.15) were significantly higher ($t(17) = -2.14$; $p < .05$) compared to RTs of patients without neglect (M = 942.08 ms, SD = 144.89).

RTs at previous distractor positions in the left hemi-field (M = 1178.57 ms, SD = 345.91) were significantly higher ($t(18) = -4.59$; $p < .01$) compared to neutral positions in the left hemi-field (M = 1060.14 ms, SD = 275.72), indicating inhibition in the left hemi-field. RTs at previous target positions in the right hemi-field (M = 927.43 ms, SD = 306.14) were significantly lower ($t(18) = -5.97$; $p < .01$) compared to neutral positions in the right hemi-field (M = 1012.38 ms, SD = 307.50), indicating facilitation in the right hemi-field.

RTs at previous target, neutral and distractor positions in the left hemi-field were significantly higher (target: $t(18) = 3.31$; $p < .01$; neutral: $t(18) = 2.23$; $p = .05$; distractor: $t(18) = 2.99$; $p < .01$) compared to RTs at respective positions in the right hemi-field.

The non-significant Neglect × Target Position and Neglect × Target Position × Side interactions (all ps > .10) do not suggest that the factor Neglect influenced the factor Target Position, thus priming effects across both hemi-fields or in a specific hemi-field.

Accuracy

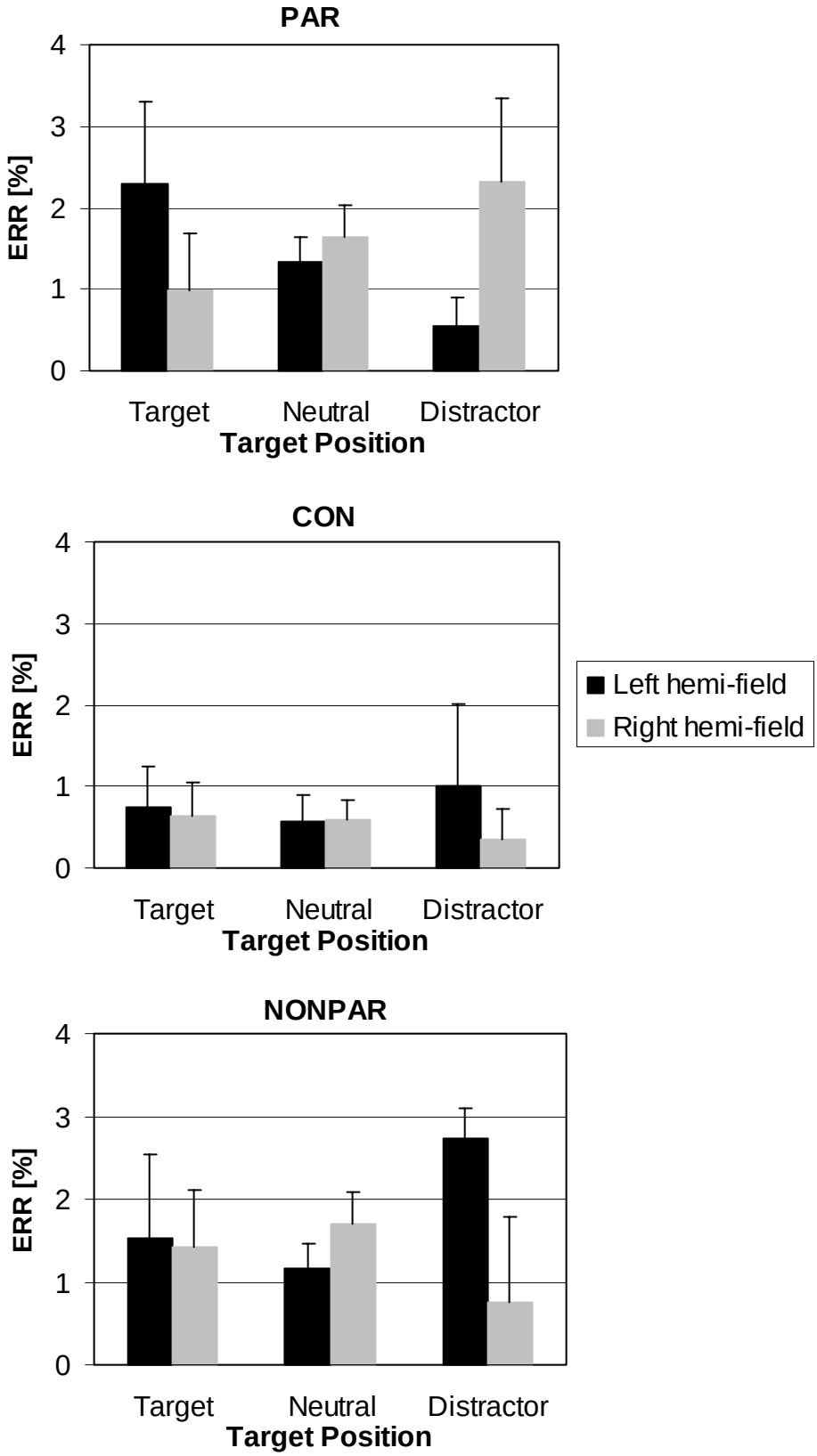


Figure 48. *Error percentage rates (ERR%) at the three target positions (target, neutral, distractor) on the left and the right side are depicted for each group (PAR, CON, NONPAR), respectively. Error bars indicate standard errors.*

Accuracy at the three target positions in the left and the right hemi-field were generally low in all groups (s. figure 48). ANOVA revealed no main effects (Group, Target Position, Side) or interactions (Group × Target Position, Group × Side, and Target Position × Side) to be significant (all *p*s > .10).

4. 3 Discussion

In the "nonrelevant distractor experiment" (11), task-nonrelevant peripheral distractor stimuli were flashed randomly on the left or on the right side of the screen between subsequent trials in order to test whether exogenously driven covert attention shifts between subsequent trials would affect location priming differentially in patients with parietal lesions compared to patients with lesions not encroaching on the parietal lobe and healthy subjects. Given the result of absent facilitation and inhibition after spatial remapping requirements induced by saccadic shifts of overt attention selectively in patients with right parietal lesions in the "spatial remapping experiment" (9) in study 2, III. chapter, p 88, disturbed priming effects in the PAR but not in the NONPAR and the CON group in the present experiment would have provided support for the assumption made by Pisella and Mattingley (2004) that covert attention shifts, in the present experiment, provoked by exogenously distractors in-between trials, induce spatial remapping requirements. On the contrary, the presence of priming effects comparably to the NONPAR and the CON group provides evidence that covert attention shifts do not induce spatial remapping requirements the way overt attention shifts do.

While accuracy data did not reveal a specific pattern, the result obtained from RTs supports the latter. Facilitatory priming was present in both hemi-fields, while inhibitory priming was present in the left, however absent in the right hemi-field. Albeit, patient groups showed higher RTs to targets in the left compared to targets in the right hemi-field (in accordance with Duncan & Desimone, 1995; Peers et al., 2005), while RTs were comparable

in both hemi-fields in the CON group, the specific pattern of priming effects was equally obtained across all groups. Crucially, the pattern was not altered in the PAR group. The presence of priming effects signifies that integration of visual information had taken place across subsequent trials. Since we assume deficient spatial remapping mechanisms in patients with parietal lesions, the presence of priming effects in the PAR group provides evidence that covert attention shifts – as provoked by peripheral distractors in the present experiment – did not induce spatial remapping requirements.

Moreover, the presence of priming effects in an equal measure in all groups also supports the assumption that the result of reduced inhibition in the PAR group as compared to the NONPAR and the CON group, obtained in the "control experiment" (10) was rather due to attentional deficits associated with parietal lesions along with the long eventless ISIs than due to deficits with spatio-temporal integration of visual information across trials.

However, although not specifically in PAR patients, peripherally flashed distractors had an influence on priming as evident from the distinct RT pattern in the present experiment as compared to the "control experiment" (10). The influence of the peripheral distractors on priming matches with findings that suggest that reflexive orienting towards peripheral exogenous cues is rather automatic and cannot be voluntarily suppressed (Jonides, 1981; Müller & Rabbitt, 1989). Here, the pattern of RTs after exogenously provoked covert attention shifts revealed disturbed inhibition in the right hemi-field. The result might be explainable in terms of an account assuming the allocation of attentional weights to objects (targets and distractors), separately for each hemi-field (Duncan, Humphreys, & Ward, 1997), and the further notion that objects with high attentional weights are processed well but interfere strongly with other objects while objects with low attentional weights are processed poorly but interfere weakly with other objects. Applied here i.e.: Objects in the left might have had lower attentional weights than objects in the right hemi-field (note that there was a tendency for lower RTs after the peripheral distractors were presented on the right compared to when they

were presented in the left side of the screen). Higher attentional weighting of objects within the right hemi-field might have led to higher interference with objects within this hemi-field, reflected by the lack of inhibition in the right hemi-field.

The assumption of a spatial working memory storage capacity limitation lateralised towards the right hemi-field could be taken into account to explain the lack of inhibition. Geyer & Müller (submitted) showed that inhibitory location-based priming in a priming of pop-out paradigm does not occur with set sizes that exceed the number of two distractors. In the present experiment peripheral distractors might have led to an extension of the set size beyond the number of two distractors by virtually adding an additional distractor (the one flashed between trials). However, the notion of a working memory storage capacity limitation on the basis of previous findings (Geyer & Müller, submitted) remains quite speculative, since the briefly flashed peripheral distractors differed from the distractors in the search array: they neither occupied possible target locations nor did they occur contemporaneously with the search array.

Notwithstanding that the lateralised influence on inhibitory priming which was consistent across all groups provided evidence that exogenously driven covert attention shifts in-between trials influenced priming, the results of the present experiment did not support the assumption that exogenously provoked covert attention shifts (although operative) induce spatial remapping requirements. Contrasted on the background of the model by Pisella and Mattingley (2004) the result provided no support of the assumption that covert attention shifts (as induced exogenously) lead to an overwriting of information on the saliency map in PAR patients, and thus disturb the seamless integration of successive visual input.

The results in the present experiment apply to exogenously driven covert attention shifts. However, there is evidence that exogenous shifts of attention are driven by distinct underlying mechanisms from endogenous shifts (Müller & Rabbitt, 1989). In line with this assumption, it had been shown that key structures of the dorsal fronto-parietal attention

network were stronger activated by voluntarily (endogenously) driven covert attention shifts compared to exogenously driven covert attention shifts (Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). Furthermore, behavioural relevant peripheral distractors had been shown to activate parietal neurons stronger compared to behaviourally irrelevant distractors (Colby et al., 1995).

Hence, it is not clear whether spatial remapping might be required after voluntary (endogenous) covert shifts of attention. If so, endogenously driven attention shifts should lead to an overwriting of the saliency map in patients with right parietal lesions. Consequently, we would expect to find disturbed priming effects in a priming of pop-out task that requires voluntary shifts in-between the trials. To allow for testing the influence of endogenously driven covert attention shifts on location priming, the “relevant distractor experiment” (12) involved an endogenous component. A secondary task was conjoint with the peripherally flashed distractors. Subjects had to report verbally on which side of the screen the distractor had been flashed.

5. RELEVANT DISTRACTOR EXPERIMENT (12)

5. 1 Method

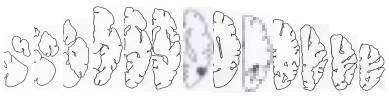
5. 1 1 Participants

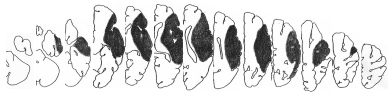
Selection criteria and procedure match the previous experiments. Patients were again assigned to two groups according to lesion site (see figure 49). 10 PAR patients and 8 NONPAR patients took part in the saccade experiment. Patients were tested at a median of 10 and within a range of 1 up to 150[6] weeks post injury. The patient groups did not differ significantly with respect to time since brain injury [$F(1, 16) = .20$; $p > .65$].

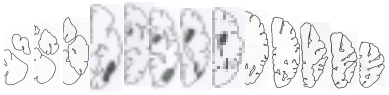
PAR:

KF 

ML 

KL 

SW 

KW 

WK 

HG 

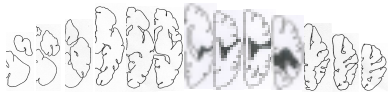
SH 

KS 

JM 

NONPAR:

GL 

HS 

[6] Patients WK and HS suffer from old lesions. They were former patients of the rehabilitation clinic.

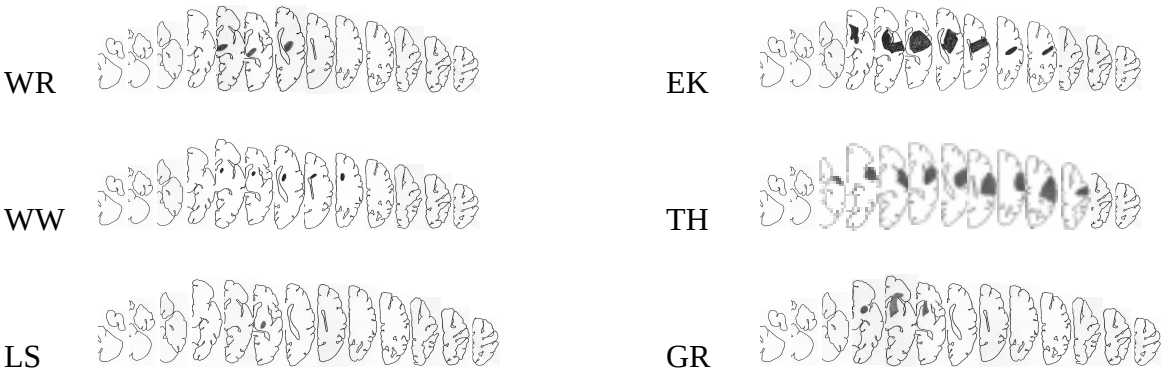


Figure 49. *Lesion reconstructions of the 18 patients*

The patient data were again compared to the data of 10 age- and education matched control subjects (CON). Patient groups did not differ significantly from the CON groups with respect to age [$F(2, 25) = .76$, $p > .45$] or education [$F(2, 25) = 1.42$, $p > .25$]. Demographical information is given in table 6. Two patients of the PAR group and one patient of the NONPAR group suffered from partial visual field loss as assessed by clinical standard diagnostic. Visual field defects are depicted in figure 50. One patient of the PAR group was left-handed.

Table 6

Group demographics and clinical information. Gender distribution, median and range for age, education, and time since injury, residual neglect

	sex (f/m)	Age [years]	Education [years]	TSI [weeks]	Injury type (CVA/Tu)	Residual neglect
CON	5/5	57.5 (26 – 66)	11.4 (9 – 13)	-	-	-
PAR	4/6	48.5 (27 – 78)	10.0 (8 – 13)	7 (1 – 105)	10/0	5
NONPAR	1/7	62.5 (34 – 82)	12.5 (8 – 13)	12 (3 – 150)	7/1	1

PAR:

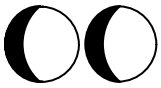
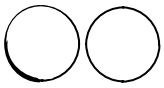
KF  KS 

Figure 50. *Visual field defects of 2 PAR patients are depicted.*

5. 1. 2 Materials

Stimuli were the same as in the “relevant distractor experiment” (6) in study 1, II. Chapter, p. 48.

5. 1. 3 Procedure

Procedure and task was the same as in the “relevant distractor experiment” (6) in study 1, II. chapter, p. 48. RTs and errors were recorded for the left and right hemi-field, separately. If necessary, break durations between experimental blocks were adjusted to patients´ individual requirements.

5. 2 Results

ANOVAS including the same factors as in the control experiment were conducted. Level of significance was 5%.

Reaction times

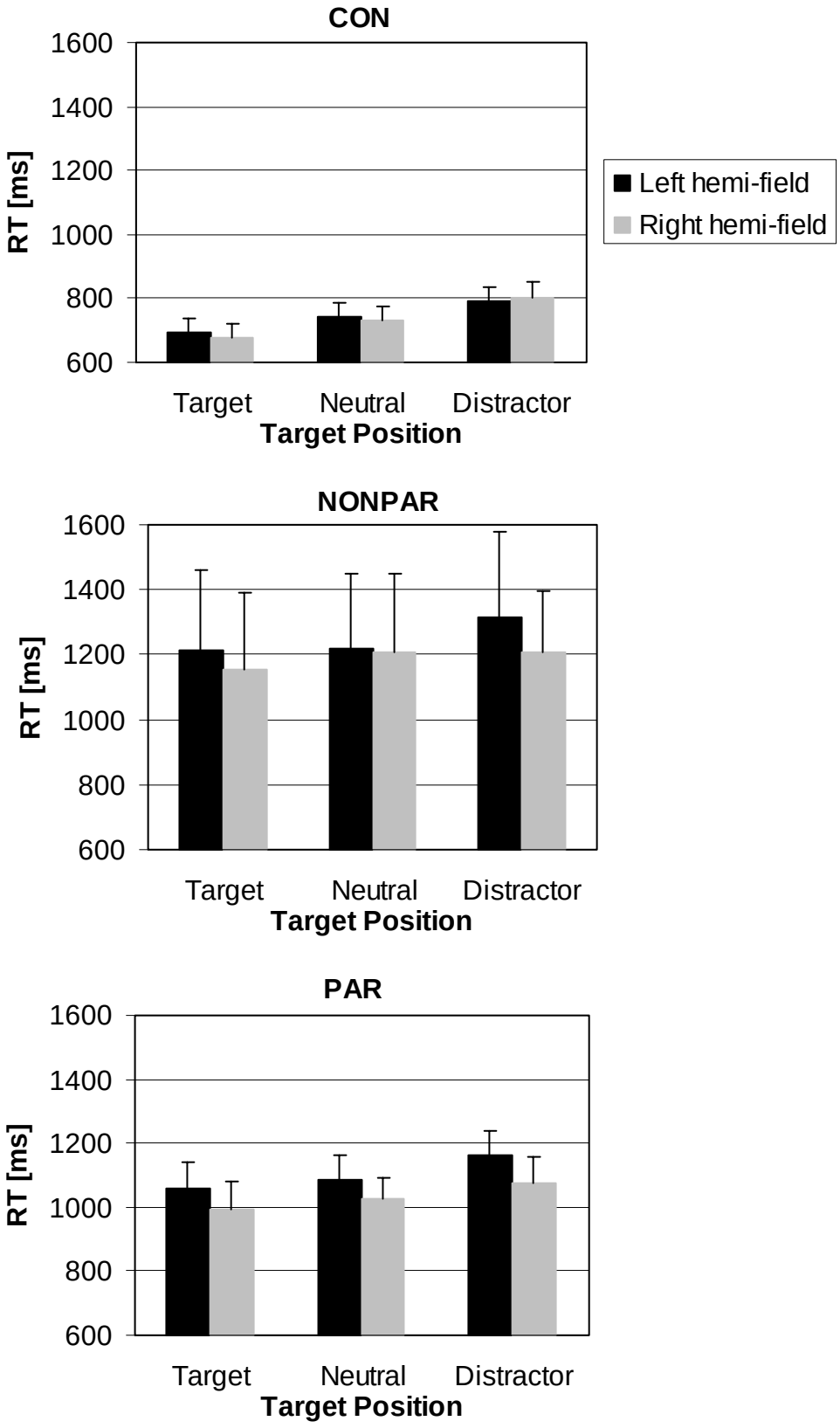


Figure 51. *Mean Reaction times (RT) at the three target positions (target, neutral, distractor) on the left and the right side are depicted for each group (CON, PAR, NONPAR), respectively. Error bars indicate standard errors.*

Mean RTs at the three target positions in the left and the right hemi-field, respectively are depicted for each group, separately, in figure 51.

ANOVA of the RTs revealed all main effects (Group: [$F(2, 25) = 5.08$, $p < .05$], Target Position: [$F(2, 24) = 32.84$, $p < .01$], and Side: [$F(1, 25) = 5.19$, $p < .05$]) to be significant.

RTs of the CON group ($M = 744.34$ ms, $SD = 151.61$) were significantly lower (PAR: t (18) = -3.11; $p < .01$; NONPAR: $t(16) = -2.70$; $p < .05$) than RTs of the PAR ($M = 1118.77$ ms, $SD = 349.65$) and the NONPAR group ($M = 1245.26$ ms, $SD = 507.05$). RTs of the patient groups did not differ significantly ($p > .50$) from each other.

RTs at previous target positions ($M = 975.41$ ms, $SD = 415.30$) were significantly lower (t (27) = -4.63; $p < .01$) and significantly higher ($t(27) = -5.35$; $p < .01$) at previous distractor positions ($M = 1070.89$ ms, $SD = 394.45$) compared to neutral positions ($M = 1017.26$ ms, $SD = 401.66$), indicating facilitation and inhibition (depicted in percent for all groups in figure 52).

RTs of targets in the left hemi-field ($M = 1041.86$ ms, $SD = 422.85$) were significantly higher ($t(27) = 2.21$; $p < .05$) than RTs in the right hemi-field ($M = 1000.51$ ms, $SD = 387.04$).

The Group × Target Position, Group × Side, Target Position × Side, and Group × Target Position × Side interaction were non-significant (all *p*s > .15).

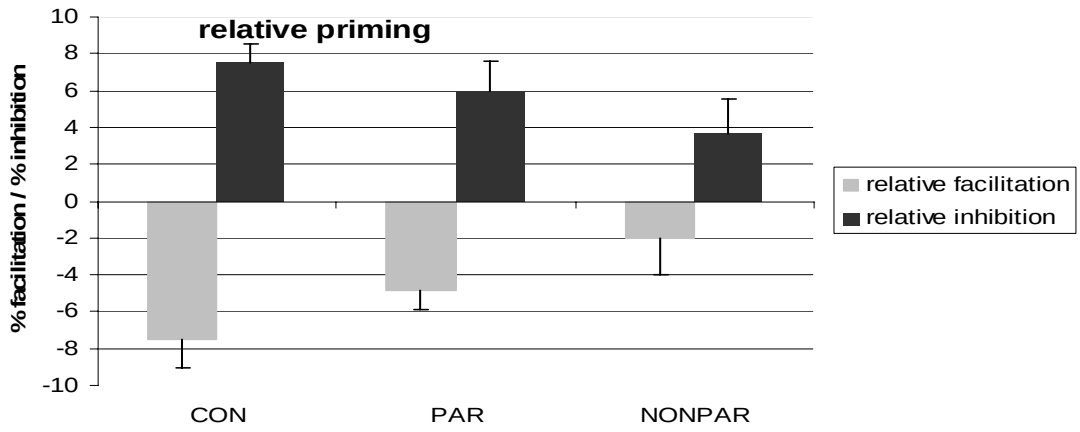


Figure 52. *Relative facilitation and inhibition in the three groups is depicted. Error bars indicate standard errors.*

Influence of the presentation side of the peripheral distractor

To test whether the different presentation sides of the peripheral distractors that triggered covert attention shifts endogenously influenced priming effects, ANOVAs analogously to the "nonrelevant experiment" (11) were conducted.

Influence of the peripheral distractor in the left and the right hemi-field

ANOVA revealed the main effects Group [$F(2, 25) = 4.35$; $p < .05$; s. above for further results], Target Position [$F(2, 24) = 12.85$; $p < .01$; s. above for further results], and Distractor Side [$F(1, 25) = 11.78$; $p < .01$] to be significant.

RTs after the peripheral distractor was flashed in the left hemi-field (M = 1049.83 ms, SD = 405.83) were significantly higher ($t(27) = 3.65$; $p < .01$) than RTs after the distractor was flashed in the right hemi-field (M = 1016.33 ms, SD = 390.21).

Further two-way and the three-way interaction (including those with the factor Distractor Side) were non-significant. (all ps > .15), indicating that priming effects were not affected by the presentation side of the peripheral distractors.

Influence of the peripheral distractor in the ipsi- and the contra-lateral hemi-field

ANOVA revealed the main effects Group (s. above), Target Position (s. above), and relative Distractor Side [$F(1, 25) = 8.90$; $p < .01$] to be significant.

RTs of targets after the peripheral distractor was flashed in the ipsi-lateral hemi-field (M = 1037.95 ms, SD = 409.04) were significantly higher ($t(27) = 2.93$; $p < .01$) than RTs of targets after the distractor was flashed in the contra-lateral hemi-field of the target (M = 1004.42 ms, SD = 397.79).

Further two-way and the three-way interaction (including those with the factor Distractor Side) were non-significant (all ps > .30), indicating that priming effects were not affected by the relative presentation side of the peripheral distractors.

Influence of neglect

Furthermore, a potential influence of neglect on priming was analysed. 6 out of 18 patients (5 out of 10 PAR and 1 out of 8 NONPAR patients) who participated in the current experiment suffered from residual mild neglect. Analogously to the previous experiments contingent contribution of neglect was calculated using an ANOVA with corresponding factors as in the previous experiments.

ANOVA revealed the main effects of Target Position [$F(2, 15) = 11.01$; $p < .01$] and Side [$F(1, 16) = 7.82$; $p < .05$] to be significant.

RTs were significantly lower ($t(17) = -2.83$; $p < .05$) at previous target positions (M = 1134.24 ms, SD = 432.36) and significantly higher ($t(17) = -3.47$; $p < .01$) at previous distractor positions (M = 1221.24 ms, SD = 407.44) compared to neutral positions (M = 1169.49 ms, SD = 420.14).

RTs of targets in the left hemi-field (M = 1207.36 ms, SD = 436.41) were significantly higher ($t(17) = 2.38$; $p < .05$) compared to RTs of targets in the right hemi-field (M = 1142.62 ms, SD = 407.11).

The main effect of Neglect and further two-way and the three-way interaction (including those with the factor Neglect) were non-significant (all ps > .15), indicating that results in the present sample were not influenced by the presence or absence of neglect.

Accuracy

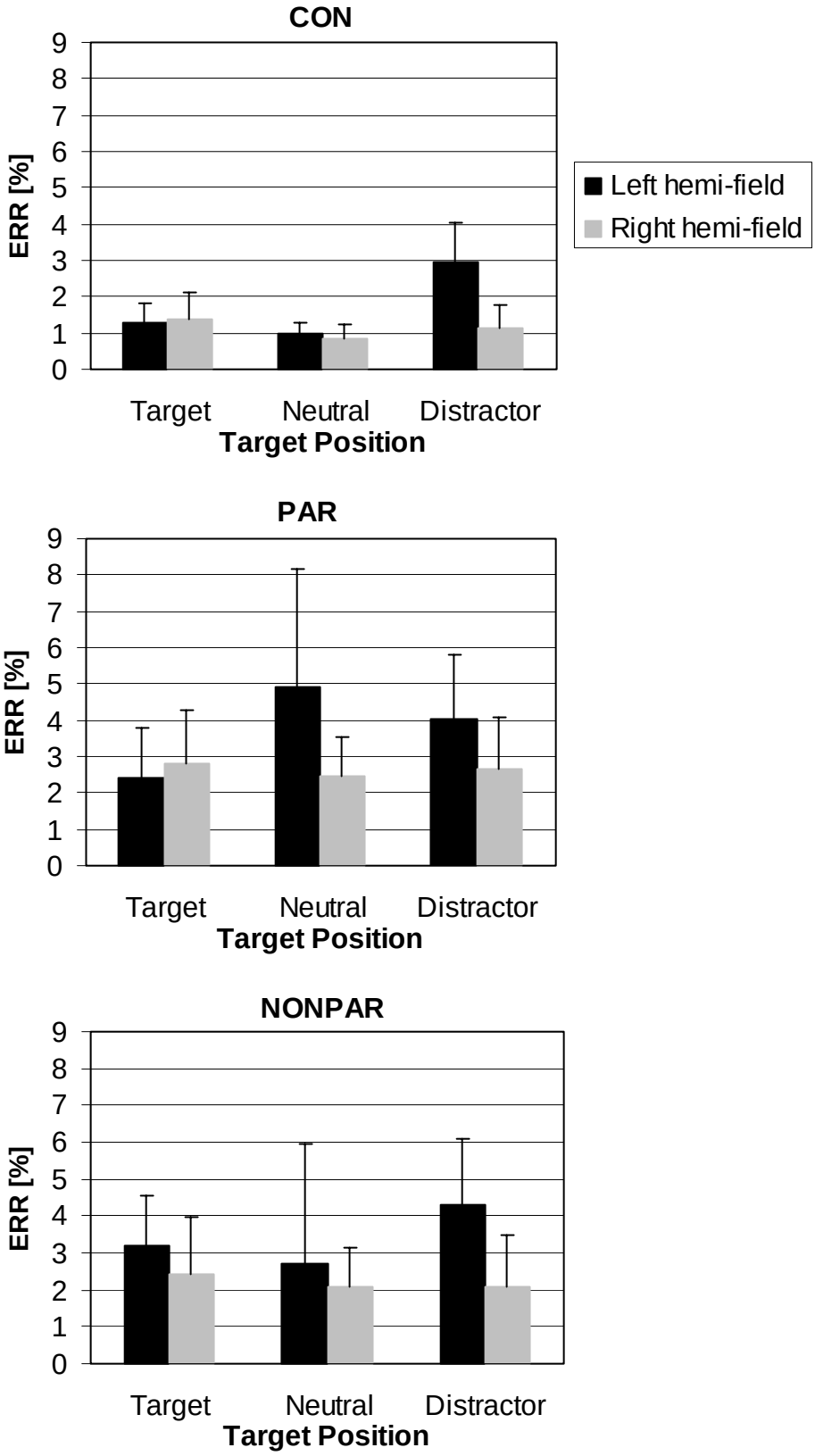


Figure 53. *Error percentage rates (ERR%) at the three target positions (target, neutral, distractor) on the left and the right side are depicted for each group (PAR, CON, NONPAR), respectively. Error bars indicate standard errors.*

Err% of all groups at the three target positions in the left and the right hemi-field are depicted in figure 53.

ANOVA revealed a marginally significant main effect Side ($p < .07$) and a marginally significant Target Position × Side ($p < 09$) interaction. This interaction occurred because err% were significantly higher at pervious distractor positions in the left ($M = 4.19$ % ; $SD = 4.44$) compared to the right hemi-field ($M = 1.83$ %; $SD = 3.68$).

The main effects Group and Target Position as well as the Group × Target Position, Group × Side, and Group × Target Position × Side interaction were non-significant (all $ps > .15$).

5. 3 Discussion

As previously shown, priming effects were not longer present in patients with right parietal lesions after saccadic shifts of overt attention ("spatial remapping experiment"; study 2, III. chapter, p. 88), while they were still present after endogenously driven covert shifts of attention ("nonrelevant distractor experiment").

The current experiment was designed to test the influence of endogenously driven covert attention shifts on priming effects in order to obtain evidence from patients with right parietal lesions whether (in contrast to exogenously) endogenously driven attention shifts would entail spatial remapping requirements. In-between subsequent trials, subjects had to indicate verbally whether a distractor had been flashed on the left or on the right side of the screen. Provided that endogenously driven covert attention shifts would induce spatial remapping requirements we would- in accordance to the model suggested by Pisella and Mattingley (2004) – have expected reduced or absent priming in the PAR group as compared to the NONPAR and the CON group due to an overwriting of information on the saliency map along with each attentional shift. In contrast, we expected preserved priming effects in

the PAR group, comparable to those in the NONPAR and the CON group, provided that no spatial remapping is required after endogenously shifts of covert attention.

The results support the latter. RTs revealed a stable pattern of facilitation and inhibition present in all groups, while accuracy did not provide particular information. The presence of priming effects indicates spatio-temporal integration of visual information across subsequent trials despite endogenous shifts of covert attention in-between trials. Crucially, priming effects were not altered in the PAR group as compared to the NONPAR and the CON group. Given the evidence that patients with right parietal lesions exhibit deficits in spatial remapping, and thus would have failed to successfully integrate visual information of subsequent trials, if spatial remapping would have been required in the present experiment, the result suggests that endogenously driven covert shifts of attention do not induce spatial remapping requirements.

Analogously to the result of present priming effects in an equal measure in all groups obtained in experiment 11, the same result in the present experiment strengthens the support for the assumption that the result of reduced inhibition in the PAR group as compared to the NONPAR and the CON group, obtained in the "control experiment" (10) was rather due to attentional deficits associated with parietal lesions along with the long eventless ISIs than due to deficits with spatio-temporal integration of visual information across trials.

However, peripherally flashed distractors had an influence, although not specifically in the PAR group but consistently across all groups, and furthermore not on priming effects but on the lateralisation of overall RTs. RTs were lower after the peripheral distractor had been flashed within the right compared to when it had been flashed within the left hemi-field, thus the tendency of a respective result obtained with exogenously covert attention shifts in the "nonrelevant experiment" (11) was more pronounced in the present experiment. Moreover, the RTs of targets which occurred in the ipsi-lateral compared to the contra-lateral hemi-field were lower. Latter finding is in line with the finding of facilitated processing of targets in the

hemi-field previously alerted (i.e. temporally enhanced in responsiveness) by a spatially valid cue with long intervals between cue and target stimulus (Posner & Cohen, 1984).

6. Conclusion

We tested whether spatial remapping would be required after covert shifts of attention as it is after overt shifts of attention with the parietal lobe crucially involved as assumed by the model of Pisella and Mattingley (2004). To that end, we tested the integrity of spatio-temporal integration of visual information by means of location-based priming in a priming of pop-out paradigm (Maljkovic & Nakayama, 1996). Provided covert shifts of attention induce spatial remapping requirements we would have priming effects expected to be disturbed in patients with right parietal lesions.

In three experiments facilitatory and inhibitory priming effects were analysed in healthy subjects and patients with right-hemispheric lesions with and without parietal involvement. In the “control experiment” (10) no attention shifts were induced in-between subsequent trials. In the “nonrelevant distractor” (11) and “relevant distractor experiment” (12) covert attention shifts were induced by peripheral distractors exogenously and endogenously, respectively.

Results obtained in the RT data of the experiments provide evidence that covert attention shifts do not induce spatial remapping requirements. Basically, facilitation and inhibition was significantly present in all groups and in all experiments, indicating spatio-temporal integration of visual information across subsequent trials.

In the “control experiment” (10), facilitation and inhibition was significantly present in all groups however, inhibition was significantly reduced in the PAR group as compared to the NONPAR and the CON group. The diminution of inhibition (as the less endurable component across time compared to facilitation) was presumably resulting from attention problems often

associated with parietal lesions (e.g. Pardo et al., 1991) during the long eventless ISIs rather than from deficits of spatio-temporal integration of visual information across trials. This assumption was supported by the results obtained in experiment 11 and 12, when peripheral distractors were presented during the ISIs, thus time during the ISIs was not longer eventless. Priming effects were then present to an equal measure in all groups.

These results of equal presence of priming effects in the PAR groups as compared to the NONPAR and the CON group in experiment 11 and 12, after covert shifts of attention in-between the trials, indicate that successful integration of visual information across trials had been taken place in these patients despite covert attention shifts. As evident from the "spatial remapping experiment" (9), study 2, III. chapter, p.88, location priming is not preserved after saccadic shifts of overt attention in patients with right parietal lesions. Reciprocally, preserved facilitation and inhibition after covert attention shifts in the PAR group can be taken as evidence that covert attention shifts do not induce spatial remapping requirements the way overt attention shifts do.

Covert attention shifts, exogenously and endogenously provoked in the "nonrelevant distractor" (11) and the "relevant distractor experiment" (12), respectively, influenced RTs but not specifically in the PAR group. In the "nonrelevant distractor experiment" (11) priming effects were altered consistently across all groups. While both priming effects were present in the left, inhibition but not facilitation was absent in the right hemi-field, explainable in the framework of an account assuming the allocation of attentional weights to objects (targets and distractors), separately for each hemi-field (Duncan et al., 1997), and the assumption that objects with high attentional weights are processed well but interfere strongly with other objects while objects with low attentional weights are processed poorly but interfere weakly with other objects. In the "relevant distractor experiment" (12), RTs were lateralised contingent with the presentation side of the peripheral distractors, lower after the peripheral distractor had been flashed within the right compared to when it had been flashed within the

left hemi-field, and lower after flashes in the ipsi-lateral compared to the contra-lateral hemi-field. Latter finding is consistent with the finding of facilitated processing of targets in the hemi-field previously alerted by a spatially valid cue with long intervals between cue and target stimulus (Posner & Cohen, 1984).

Crucially, the impact of exogenously and endogenously driven covert attention shifts on the RTs which was consistently obtained across all groups, indicates efficiency of the peripheral distractors for the purpose of distracting attention, and thus provides evidence that actually covert attention shifts had taken place. However, a differential effect on priming in the PAR group as compared to the NONPAR and the CON groups as it has been obtained after overt shifts of attention stayed away.

Although functionally (e. g. Deubel & Schneider, 1996) and on the neuronal level (Fink et al., 1997; Corbetta et al., 1998; Nobre et al., 2000; Beauchamp et al., 2001; Hafed & Clark, 2002; Ignashchenkova et al., 2004; Goldberg et al., 2006) tightly linked it has been shown that overt and covert attention shifts are dissociable from one another (Posner et al., 1982; Khan et al., in press) and can have differential impacts in perception tasks (Cox et al., 2005; Melcher, 2007) and on neurophysiological mechanisms (Duhamel et al., 1992a). Regarding neurophysiological findings in monkeys, the assumption that covert shifts of attention induces spatial remapping requirements (Pisella & Mattingley, 2004) the way overt shifts do, is not supported. LIP neurons were found to remap stimuli at post-saccadic locations in anticipation of saccades and according to memory traces at locations where stimuli were no longer present (Duhamel et al., 1992b; Colby et al., 1995). For both types of remapping in LIP neurons (intended) eye movements were found to be essential while covert attention shifts without intended saccades failed to elicit remapping. In humans the parietal lobe is supposed to play a crucial role for spatial remapping presumably due to similar characteristic behaviour of parietal neurons (Heide et al., 2001; Merriam et al., 2003; Bellebaum et al., 2005; Heiser et al., 2005; Berman et al., 2007; Morris, 2007).

Recently, Vasquez and Danckert (2008) investigated the influence of overt and covert shifts of attention on the performance in a spatial working memory task. What they found was a greater cost after shifts of attention to the right compared to the left hemi-field and greater costs after covert compared to overt shifts of attention. Their interpretation that the costs on working memory performance were attributable to spatial remapping after covert and overt attention shifts was based on findings about a right hemispheric dominance for attentional and spatial processing, and the assumption made by Pisella and Mattingley (2004) that spatial remapping mechanisms actually operate after both, overt and covert attention shifts. Several factors might contribute to the difference between the results obtained by Vasquez & Danckert (2008) and the results obtained in the present study. The study by Vasquez & Danckert (2008) was designed to investigate memory-based remapping in healthy subjects. Moreover, the task applied to investigate the influence of spatial remapping after covert attention shifts involved spatial displacements of the search arrays. It is possible that, firstly, memory-based remapping might differ, or involve additional mechanisms compared to the spatio-temporal integration processes we focused on in our study. The paradigm used in our experiments provided a method to measure spatio-temporal integration directly by focusing on spatio-temporal integration of visual information. Secondly, because Vasquez & Danckert (2008) investigated healthy subjects behaviourally they are not able to draw conclusions about brain areas involved, e.g. that parietal lobe functions contributed to their results. In contrast, our study explicitly addressed spatial remapping processes in the parietal lobe. We specifically approached the question whether the parietal lobe might provide the neural substrate involved in spatial remapping after covert attention shifts as assumed in the model by Pisella and Mattingley´s (2004). As the authors point out, “further electrophysiological studies should focus on possible remapping processes across covert shifts of attention” (p. 197). Results of the present study suggest that these processes (in contrast to spatial remapping after saccadic shifts of attention) do not operate in the parietal cortex.

Most importantly, the task applied to investigate the influence of covert attention shifts on spatial remapping in the Vasquez and Danckert (2008) study involved a spatial displacement of the search array, while our paradigm allowed for disentangling the impact of covert attention shift from the impact of spatial displacement of the visual search array, and thus addressed the hypothesis that spatial remapping after covert attention shifts consists in the refreshing rather than in re-locating of information on the saliency map.

Taken together, the results of the present study do not support the idea that spatial remapping mechanisms in the parietal lobe operate in order to re-fresh information on the saliency map after shifts of covert attention. However, we can not conclude that respective mechanisms operate in different structures than the parietal cortex, or whether spatial remapping mechanisms operate after covert attention shifts along with displacements of spatial search arrays.

V. CHAPTER

GENERAL CONCLUSION

We investigated spatial remapping mechanisms which are assumed to accomplish integration of visual information across space and time (Pisella & Mattingley, 2004) by the use of a priming of pop-out paradigm (Maljkovic & Nakayama, 1996). Location-based priming effects, facilitation and inhibition, are supposed to indicate the integrity of spatio-temporal integration of visual information across subsequent trials (Chun & Nakayama, 2000). We analysed them in three studies.

In study 1 we showed that location-based priming effects outlive spatial shifts of attention in healthy subjects. To test whether priming effects would outlive saccadic shifts of overt attention, subjects had to re-fixate the fixation cross in turns on the left and on the right side of the monitor between subsequent trials.

Subjects showed priming effects, facilitation and inhibition, in two separate experiments at post-saccadically retinotopic and spatiotopic locations, respectively. Facilitation obtained in both experiments was comparable among each other and comparable to facilitation obtained in a control experiment which required no attentional shifts. Inhibition was smaller in magnitude compared to facilitation in the same experiments, respectively, and compared to inhibition in the control experiment.

The differential impact of overt shifts of attention on facilitation and inhibition, respectively, and in particular, the scaling down of inhibition but not of facilitation is in accordance with the assumption that firstly, facilitatory and inhibitory priming effects, reflect two different mechanisms to sub-serve different components in visual search, and secondly, that inhibition is the more vulnerable component compared to facilitation (Maljkovic & Nakayama, 1996; Geyer et al., 2007; Geyer & Müller, submitted).

To test whether priming effects would outlive covert shifts of attention subjects´ attention was distracted between subsequent trials while they maintained fixation. Both facilitatory and inhibitory priming effects were equally present in two separate experiments

after exogenous and endogenous attention shifts, respectively. Both effects were comparable in magnitude to those obtained in the control experiment without attention shifts.

The presence of priming effects despite interfering overt and covert attention shifts was taken as evidence that processes that integrate visual information along with attention shifts operate flawlessly in healthy subjects. However, firstly, our results support the notion of two different underlying mechanisms for facilitation and inhibition, and, secondly, two different ways of "outliving" overt and covert shifts of attention, respectively.

In order to investigate the nature of spatial remapping more closely we applied the experiments used in study 1 in two further studies. In study 2 and 3 we compared performance of healthy subjects to the performance of patients with right-hemispheric lesions with and without parietal involvement.

The aim of study 2 was to test whether the parietal cortex provides the neural correlate of spatial remapping as assumed by Pisella and Mattingley (2004). We analysed priming effects after overt shifts of attention at postsaccadically retinotopic and spatiotopic locations, and in the control experiment without attention shifts. The separate measurement of priming at postsaccadically retinotopic ("saccade experiment") and spatiotopic ("spatial remapping experiment") locations, provided the opportunity to disentangle the influence of two factors which are often confounded in experiments assessing spatial remapping abilities (e.g. Heide et al., 1995). Here, we disentangled the influence of saccades only ("saccade experiment") from the influence of spatial remapping deficits ("spatial remapping experiment") on location priming effects. We found preserved priming effects, facilitation and inhibition across all groups in the "control experiment" (7), when no interfering events occurred between subsequent trials. The effect of facilitation was even enhanced in the PAR group as compared to the NONPAR and the CON group. Furthermore, we obtained facilitation and inhibition at retinotopic locations after overt attention shifts in the "saccade experiment" (8). In the "spatial remapping experiment" (9), we obtained, in accordance with the results in study 1, facilitation

and inhibition at spatiotopic locations in healthy subjects. Moreover, in accordance with the assumption that the crucial structure for remapping is the parietal cortex, and that impairments of spatial remapping mechanisms are not an unspecific deficit occurring after right-hemispheric lesions, we found facilitation and inhibition in the NONPAR group. However, patients with right parietal lesions showed neither facilitation nor inhibition. This interesting result provides evidence that subsequently presented visual information was not integrated across trials when saccadic shifts of overt attention were required in-between trials. Since the integration is assumed to be accomplished by spatial remapping mechanisms, our results support the assumption that the parietal cortex is a brain structure which is involved in spatial remapping. Furthermore, given that priming effects play a crucial role in supporting visual search performance, our results support the assumption by Pisella and Mattingley (2004) that spatial remapping deficits might contribute to visual search impairments often demonstrated by patients with right parietal lesions. A lack of facilitation e.g. might contribute to explain the random scanpath found in patients with parietal lesions (in contrast to goal-directed saccades in healthy subjects) while looking for a target when the location of the target is already known from a preview display (Shimozaki et al., 2003). A lack of inhibition might contribute e.g. to explain the phenomenon of revisiting behaviour exhibited by patients with parietal lesions (Pisella et al., 2004).

The aim of study 3 was to test the model's assumption that spatial remapping is required after spatial shifts of covert attention. As assumed by the model of Pisella and Mattingley (2004) spatial remapping mechanisms located in the parietal lobe operate after covert shifts of attention. Remapping processes after covert (as compared to overt) shifts of attention had been suggested to consist in refreshing rather than in a relocating of activity foci on the saliency map. In a recent study by Vasquez and Danckert (2008) that supports the assumption that covert attention shifts induce spatial remapping requirements, the task applied involved spatial displacements of the search arrays. Thus, in terms of the model by Pisella and

Mattingley (2004) relocation and refreshing of information on the saliency map might have been confounded. The paradigm here allowed disentangling the influence of spatial displacements of the search arrays from the influence of covert attention shifts.

Given that the result in the “spatial remapping experiment” (9), study 2 (p. 88), suggests spatial remapping deficits in patients with right parietal lesions, we expected to obtain evidence from patients with parietal lesions whether covert attention shifts would induce spatial remapping requirements or not. Thus again, we compared priming effects of patients with right parietal lesions to those of patients with right-hemispheric lesions without parietal involvement, and healthy subjects. We established the “control experiment” (10) with a longer ISI compared to the “control experiment” (7) used in study 2. The long ISI was needed in order to have time to flash peripheral stimuli that distract attention in-between trials in the “nonrelevant distractor” (11) and the “relevant distractor experiment (12). In the “control experiment” (10) without attention shifts between subsequent trials, both facilitation and inhibition was significantly present in all groups. However, inhibition was significantly diminished in the PAR group as compared to the NONPAR and the CON group. Rather than attributable to spatial remapping deficits which were of interest in the current study, the attenuation of inhibition might have occurred due to attention problems often associated with right parietal lesions during the long ISI. Given that the presence of facilitation and inhibition provided evidence for a basically successful integration of visual information across trials, the purpose of the “control experiment” (10) could be considered to be not derogated. Moreover, it was expected that – provided that covert attention shifts might not disturb priming in the PAR group – the reduction of inhibition found with the long eventless ISI would not occur when peripheral distractors were presented during the ISI. This was exactly what was found. Although peripheral distractors had a lateralised influence, this influence was not specific for the PAR group but consistent across all groups. In particular, after exogenously driven shifts of covert attention, facilitation and inhibition was present in the left while facilitation but not

inhibition was present in the right hemi-field. Crucially, the lack of inhibition in the right-hemi-field occurred in all groups, and thus was not attributable to spatial remapping deficits. After endogenously driven shifts of covert attention, facilitation and inhibition was equally present in all groups. Crucially, the presence of priming effects in the PAR group, comparably to the NONPAR and the CON group, provided evidence that spatio-temporal integration was accomplished by those patients. Since it is assumed that due to deficient spatial remapping mechanisms, priming effects would not have been present provided that covert shifts of attention would have induced spatial remapping requirements, the presence of priming effects can be taken as evidence, that covert shifts of attention do not entail spatial remapping.

Hence, the results of study 3 are not in accordance with the model's assumptions that covert shifts of attention would induce spatial remapping requirements with the spatial remapping mechanisms anatomically located in the parietal lobe.

To summarize, results in study 2 support the assumption of the model by Pisella and Mattingley (2004) that the right parietal lobe is crucially involved in spatial remapping, and that spatial remapping is required after saccadic shifts of overt attention. Crucial for inducing spatial remapping requirements here was the displacement of the search array ("spatial remapping experiment") rather than saccades between the trials ("saccade experiment").

Results in study 3 provided evidence that covert attention shifts per se do not induce spatial remapping requirements. More precisely, the hypothesis devised by Pisella and Mattingley (2004, p. 187) that covert attention shifts entail spatial remapping which consists in a refreshment of activities on the saliency map located in the parietal cortex is not supported by results in study 3.

However, from results in study 3, we can not rule out that there might be mechanisms that compensate for covert attention shifts which operate elsewhere than in the right parietal cortex. Furthermore, we can not conclude whether spatial remapping mechanisms operate

after covert attention shifts along with displacements of spatial search arrays (as e.g. suggested by the results obtained by Vasquez and Danckert; 2008).

The latter assumption stands particularly to reason because without (ego-centric) displacement of search arrays, spatial remapping requirements were neither induced after overt (see study 2, “saccade experiment”) nor after covert attention shifts (study 3). The crucial spatial remapping inducing elements with saccadic shifts of overt attention in study 2 were not saccades but the ego-centric displacements of the search arrays into different retinotopic coordinates.

Future prospects

Here we established a location-based priming of pop-out paradigm as a method to asses the integrity of spatio-temporal contingency. Based on theoretical assumptions provided by the model of Pisella and Mattingley (2004) we were able to draw some conclusions about the nature of mechanisms operating to accomplish this contingency.

Subsequently to the conclusions drawn from the patient studies 2 and 3 where we focused on the influence of overt and covert attention shifts, the question about the actual role of the ego-centric displacement of the search array as spatial remapping inducing element raises. We investigated the influence of overt attention shifts (study 2) on location priming within retinotopical equal but spatiotopically displaced search arrays (“saccade experiment) and vice versa, in spatiotopical equal but retinotopically displaced search arrays (“spatial remapping experiment”). Evidence from patients with right parietal lesions suggested spatial remapping requirements after retinotopically displaced search arrays. Furthermore, we investigated covert attention shifts (study 3) in two experiments (“nonrelevant distractor” and “relevant distractor experiment”) without displacements of the search arrays. Evidence from patients with right parietal lesions suggested that spatial remapping was not required. Consequently, in a next step the question should be addressed, whether displacements of the

search arrays along with covert attention shifts would induce spatial remapping requirements. To that end, another experimental modification of the paradigm established in the present studies could be applied in a similar design as in the patient studies 2 and 3. That is, performance of patients with right parietal lesions, as compared to patients with right-hemispheric lesions without parietal involvement and healthy subjects, could provide evidence whether spatial remapping would be required or not when the search arrays are presented in turns on the left and on the ride side with regard to a central fixation cross, while the participants maintain fixation, and thus shift their attention covertly in order to accomplish the search task.

Other studies should address further assumptions made within the interesting theoretical framework of the model by Pisella and Mattingley (2004).

For instance, firstly, complementary to the focus on right parietal lesions in the present patient studies, the assumption of spatial remapping deficits in patients with left parietal lesions should be addressed. To that end, priming effects in the same experiments as applied in the present studies should be analysed in patients with left parietal lesions. Their performance should be compared to the performance of patients with left-hemispheric lesions without parietal involvement, and healthy subjects. Further comparisons could then be drawn on the differences between left and right parietal involvement in spatial remapping by comparing data obtained from patients with left parietal lesions and the present data of patients with right parietal lesions.

Secondly, in study 2, we disentangled impacts of saccades from the impact of saccadic remapping. However, since our experiments required saccades from the left side to the right side of the screen and vice versa, we were not able to test the model's predictions about saccade-direction specific overwriting of information on the saliency map selectively in one hemi-field. Thus, it would be interesting to test the model's prediction that information after saccades is selectively overwritten after left parietal lesions in the contra-lateral hemi-fields

only and after right parietal lesions contra-laterally in the left hemi-field after rightward saccades, and completely after rightward saccades. To that end, the paradigm established here could be used in an experimental modification which provides search arrays and required saccades restricted in one hemi-field only.

Testable theoretical assumptions and an appropriate method might pave the way towards insights in these and many other interesting and important aspects of human visuo-spatial abilities.

Deutsche Zusammenfassung (German summary)

Wir nehmen die Welt um uns herum als stabil und räumlich kohärent wahr, obwohl sich die Bilder, die auf unserer Netzhaut eintreffen buchstäblich mit jedem „Augenblick“ ändern. Mechanismen, die zu dieser stabilen Raumwahrnehmung beitragen und uns davor bewahren, die Welt als eine Aneinanderreihung von schwankenden Einzelbildern wahrzumehmen, sind Gegenstand dieser Arbeit.

Im folgenden werden die theoretischen Kostrukte und Modellannahmen skizziert, die für das Verständnis der - dem nachfolgend - vorgestellten Studien von Belang sind.

Theoretischer Hintergrund und Modellannahmen zum räumlichen Remapping

Salienzkarte

Der begrenzten Verarbeitungskapazit unseres Gehirns Rechnung tragend, werden nur relevante Stimuli für die Weiterverarbeitung aus der Gesamtheit der auf uns einströmenden visuellen Informationen selektiert. Ein grundlegendes basal gesteuertes („bottom-up) Selektionskriterium (neben strategie- und handlungsrelevanter Selektion) für die Weiterverarbeitung von Objekten ist deren Salienz (d.h. deren inhärente Auffälligkeit). Objekte an bestimmten Positionen werden als salient (bzw. salienter im Vergleich zu anderen Objekten an anderen Positionen) wahrgenommen in Abhängigkeit ihrer Unterschiedlichkeit bzgl. ihrer visuellen Merkmalen (wie z.B. Farbe, Orientierung, Kontrast, Bewegung) im Vergleich zu den Merkmalen der Objekte an anderen Stellen (Parkhurst et al., 2002, Constantinidis et al., 2005). Merkmalsinformationen der Objekte werden auf Merkmalskarten

repräsentiert, die dann gleich darauf in eine einheitliche Repräsentation auf einer Salienzkarte zusammengeführt werden. Die Repräsentation auf der Salienzkarte stellt somit ein globales Maß für auffällige Orte in einer visuellen Szenen dar. Aufmerksamkeit wird dann zuerst an den auffälligsten Ort gelenkt (Itti & Koch, 2001). Die Aktivität an diesem Ort wird im Anschluss unterdrückt, so dass die Aufmerksamkeit an den nächstauffälligsten Ort gelenkt werden kann, an dem die Aktivität daraufhin wiederum unterdrückt wird (Itti, 2000), so dass Aufmerkskeit sequentiell (als Funktion absteigender Salienz) zu den verschiedenen Orten auf der Karte gelenkt wird. Durch die immerzu erfolgende (und durch die Salienz gelenkte) Aufmerksamkeitszuwendung zu den Orten auf der Salienzkarte entsteht eine stabile und letztendlich auch bewusste Repräsentation des Raumes.

Zwei Stufen der visuellen Verarbeitung

Die Verarbeitung hin zu einer bewussten Raumrepräsentation kann Niebur und Koch (1998) zufolge als zweistufiger Prozess beschrieben werden. In der ersten Stufe werden die elementaren Merkmale (Farbe, Orientierung, Bewegung etc.) über alle Orte in einer visuellen Szene – parallel, d.h. gleichzeitig - extrahiert und dann auf der Salienzkarte abgebildet. Das Maß der Salienz ist repräsentiert durch die Höhe der Aktivität an der Stelle auf der Salienzkarte. In der zweiten Stufe wird dann (offene und verdeckte) Aufmerksamkeit zu den verschiedenen Orten auf der Salienzkarte gelenkt. Seriell, d.h. der Reihe nach und nach dem „alles-oder-nichts-Prinzip“ werden hier nur die Objekte ausgewählt, deren Salienz (im Vergleich zur Salienz der gesamten Objekte in einer gegebenen Szene) eine bestimmte Schwelle überschreiten (d.h. deren entsprechende Aktivität auf der Salienzkarte über einer bestimmten Schwelle liegt). Diese Orte finden Eingang in eine bewusste Repräsentation des Raumes.

Räumliches Remapping

Pisella und Mattingley (2004) schlagen vor, dass räumliche Remapping-Mechanismen ihrerseits in zwei aufeinanderfolgenden Prozessen zwischen den beiden Verarbeitungsstufen der visuellen Verarbeitung (Niebur & Koch, 1998) arbeiten, um eine raum-zeitliche Kontinuität zur gewährleisten. Während des ersten Prozesses wird diejenige Information ausgewählt, deren InformationAktivität über einer bestimmten Schwelle überschreitet und deshalb vor einem Überschreiben auf der Salienzkarte geschützt wird. Die ausgewählte Information wird dann im zweiten Prozess auf der Salienzkarte – im Einklang mit Veränderungen des retinalen Abbildes (herbeigeführt durch Augenbewegungen) – re-positioniert.

Die Neuroanatomie räumlicher Remapping-Mechanismen

Neurophysiologische Befunden bei Affen, die zeigen, dass eine neuronale Raumrepräsenation im lateralen intraparielalen cortex (LIP) nur saliente bzw. verhaltensrelevante Stimuli einbeziehen, stimmen sehr gut mit den theoretischen Vorstellungen über eine Repräsentation auf einer Salienzkarte und der ersten Verarbeitungsstufe der visuellen Verarbeitung wie sie von Niebur und Koch (1998) vorgeschlagen wurde, überein. Pisella und Mattingley (2004) schlagen deswegen in ihrem Model den parietalen Cortex als neuronales Korrelat der Salienzkarte vor, in dem dann entsprechend räumliche Remapping-Mechanismen arbeiten. Aufgrund einer Reihe von experimentellen Befunden schlagen sie Strukturen des superioren parietalen cortex (SPL) als neuronales Korrelat der Salienzkarte (erste Stufe der visuellen Verarbeitung, Niebur & Koch, 1998) und Strukturen des intraparietalen Cortex (IPL) als Korrelat für die bewusste Raumrepräsentation (zweite Stufe der visuellen Verarbeitung, Niebur & Koch, 1998) vor.

Räumliche Remapping-Defizite bei Patienten mit parietalen Läsionen

Gemäß einer Repräsentation des Außenraumes im jeweils kontralateralen parietalen Cortex (Sereno et al., 2001) treten Remapping-Defizite nach Schädigungen sowohl des linken als auch des rechten parietalen Cortex auf. Gemäß der Annahme, dass die rechte Hemisphäre die Lenkung der Aufmerksamkeit in beide visuellen Felder und die linke Hemisphäre die Aufmerkskeitslenkung lediglich in das rechte visuelle Feld kontrolliert (Pisella & Mattingley), ist eine Beeinträchtung der räumlichen Remapping-Leistung nach rechten parietalen Läsionen größer als nach linken.

Nach linksparietalen Läsionen führt eine nach links und rechts gerichtete Sakkade jeweils zur Überschreibung der Information auf der jeweils contralateralen Seite der Salienzkarte. Nach rechtsparietalen Läsionen führen Sakkaden nach rechtsgerichteten Sakkaden zur einer Überschreibung der Information auf der linken Seite, während nach links gerichtete Sakkaden ein Überschreiben der Information auf der gesamten Salienzkarte zur Folge hat. (siehe Pisella & Mattingley, 2004, Abbildung 8, p. 192). Information, die auf der Salienzkarte überschrieben wurde, steht in der Folge nicht mehr für eine weitere Verarbeitung zur Verfügung und wird folglich auch nicht mehr bewusst repräsentiert.

Unterstützung für diese Modellannahme findet sich in Studien, die die Durchführung von Sakkaden bei Patienten mit parietalen Schädigungen in „Double-step“-Sakkaden-Aufgabe erfasst haben (Duhamel et al., 1992a; Heide et al., 1995). Die Aufgabe verlangt die Durchführung zweier hintereinanderfolgender Sakkaden zu zwei verschiedenen Zielpunkten. Die Zielpunkte leuchten vor Beginn der Aufgabe nur kurz auf und sind nicht sichtbar während der Durchführung der Aufgabe. Die erste Sakkade kann unter Zugrundelegung der retinalen Koordinaten vom Startpunkt zum ersten Zielpunkt durchgeführt werden. Die korrekte Durchführung der zweiten Sakkade, jedoch muss unter Einbezug des „Weges“ der ersten Sakkade erfolgen. Die räumlichen Koordinanten für den neuen Startpunkt (d.h. den Zielpunkt der ersten Sakkade) hin zum zweiten Zielpunkt müssen folglich nach Durchführung der ersten

Sakkade nach Durchführung von räumlichem Remapping berechnet werden. Patienten mit links parietalen Läsionen zeigten intakte erste und zweite Sakkaden, wenn sich Startpunkt und Zielpunkte für die Sakkaden im selben visuellen Feld befanden. Patienten mit rechts parietalen Läsionen jedoch verfehlten den Zielpunkt der zweiten Sakkade, wenn sich beide Zielpunkte im rechten visuellen Feld befanden (Heide et al., 1995).

Beitrag räumlicher Remapping-Defizite zu Störungen der visuellen Suche bei Neglect

Eine Vielzahl von Symptomen und Phänomenen, die im Rahmen des sehr heterogenen Neglect-Syndroms, einer neurologischen Erkrankung, die häufig nach rechtsseitiger, v.a. parietaler Hirnschädigung, auftritt, lassen sich nicht in vollem Umfang von gängigen Theorien erklären. Darunter der „ipsiläsionale“ Neglect, der auftritt, nachdem Patienten die Aufmerksamkeit ins linke visuelle Halbfeld gelenkt haben und entsprechend in Linienhalbierungsaufgaben untypischerweise die Mitte zu weit links einschätzen (Mattingley et al., 1993) oder Stimuli auf der rechten Seite nicht berichten. Desweiteren das Phänomen des wiederholten Absuchens bereits abgesuchter Stellen auf der rechten Seite (Husain et al., 2001), oder das wiederholte Durchstreichen von Linien auf der rechten Seite in Linienhalbierungsaufgaben. (Rusconi et al., 2002) oder desorganisierte Suchstrategien, gekennzeichnet durch ziellose Blickbewegungen (Wojciulik et al., 2001).

Pisella und Mattingley (2004) weisen darauf hin, dass eine Annahme zugrundeliegender räumlicher Remapping-Defizite diese Phänomene erklärbar macht. Desweiteren könnten Remapping-Defizite erklären, warum Neglectpatienten (meist contraläsional) vernachlässigte Stimuli nicht bewusst wahrnehmen.

Spatial remapping und die Grenzen bei Gesunden

Das Phänomen der Veränderungsblindheit (e.g. Beck et al., 2001), d.h. der Unfähigkeit – bei Gesunden – unter bestimmten Umständen Veränderungen in visuellen

Szenen zu bemerken, reflektiert Pisella und Mattingley (2004) zufolge ebenfalls wie Neglect bei Patienten die Natur räumlicher Remapping-Mechansimen, in dem Sinne, dass visuelle Information zwar in primären visuellen Verarbeitungsarealen ankommt, jedoch ein Teil der Information nicht bewusst abrufbar ist.

Im Falle der Veränderungsblindheit, die für Elemente an Stellen, zu denen keine Aufmerksamkeit gelenkt wurde, auftritt, wird die entsprechende visuelle Information nicht auf der Salienzkarte repräsentiert und ist in der Folge nicht in einer bewussten Repräsentation verfügbar.

Die Rolle offener und verdeckter Aufmerksamkeit

Pisella und Mattingley (2004) nehmen demnach an, dass räumliches Remapping sowohl nach offener als auch verdeckter Aufmerksamkeitsablenkung erforderlich ist. Die Annahme für Remapping-Anforderungen nach verdeckter Aufmerksamkeit wird einerseits gestützt durch die empirische Beobachtung, dass Veränderungsblinkheit auch nach verdeckter Aufmerksamkeitsverschiebung auftritt, zum anderen durch die enge Verknüpfung von offener und verdeckter Aufmerksamkeit auf neuronaler Ebene (Corbetta et al., 1998).

Die Annahme ist, dass Aktivitäten auf der Salienzkarte durch räumliche Remapping-Prozesse nach offener Aufmerksamkeitsverschiebung re-positioniert werden, während sie nach verdeckter Aufmerksamkeitsablenkung aufgefrischt werden.

Priming of Pop-out zur Erfassung raum-zeitlicher Integrationsleistungen

Um räumliche Remapping-Mechanismen zu erfassen und einige der Annahmen in Pisella und Mattingleys (2004) Modell zu testen, wurden Positionsprimingeffekte in einem Priming of pop-out Paradigma (Maljkovic & Nakayama 1994, 1996, 2000) analyisiert. Ein solches Paradimga erlaubt den Einfluss visueller Erfahrung aus einem vorherigen Durchgang

in einem aktuellen Durchgang zu messen. Die Aufgabe ist einen Pop-out-Zielreiz unter heterogen Distraktoren zu finden. Ein Pop-out-Zielreiz unterscheidet sich von den Distraktoren in einem einzigen Merkmal (z. B. Farbe), und „popt“ deswegen aus dem Display. Der Pop-out-Effekt basiert auf der extremen Salienz des Zielreizes, der eine extrem schnelle Aufmerksamkeitszuwendung zu Folge hat.

Wie man weiß, ist die Reaktionszeit (RZ) zum Zielreiz beeinflussbar durch dessen Position im Vergleich zur Position in einem vorherigen Durchgang (Maljkovic & Nakayama, 1996). Auf Zielreize, die an vorherigen Zielreizpositionen präsentiert werden, wird schneller und fehlerfreier reagiert (Erleicherung), als auf Zielreize, die an vorherigen Distraktorpositionen präsentiert werden, auf welche entsprechend langsamer und öfter fehlerhaft reagiert wird.(Hemmung). In unseren Experimenten haben wir Erleichertung und Hemmung relativ zu einer Baseline, d.h. RZ auf Zielreize, die an neutralen (vormals leeren) Positionen präsentiert wurden.

Die Präsenz von Priming-Effekten kann als Indiz für erfolgreiche raum-zeitliche Integration aufeinanderfolgender visueller Information gewertet werden (Chun & Nakayama, 2000). Erfolgreiche Information basiert – dem Modell folgend – auf erfolgreichem räumlichen Remapping.

In den Experimenten in den nachfolgend vorgestellten Studien wurden aufeinanderfolgende visuelle Suchanordnungen präsentiert, die jeweils einen roten diamantförmingen Zielreiz unter zwei grünen diamantförmingen Ablenkerreizen zeigten. Ziel- und Distraktorreize hatten unabhängig voneinander und zufällig oben oder unten eine flache Seite. Die Aufgabe war, so schnell und so genau wie möglich, mittels Tastendruck (oben oder unten) anzuzeigen, wo (oben oder unten) die flache Seite des roten Zielreizes war.

Zusammenfassung der Studien 1 bis 3

Wir analysierten Primingeffekte - und somit die Fähigkeit visuelle Information aus aufeinanderfolgenden Durchgängen zu integrieren - in drei Studien.

Aus vorherigen Studien, die Priming in Bedingungen untersuchten, die keine Aufmerksamkeitsverschiebungen (weder offen noch verdeckt) zwischen den Durchgängen erforderlich machten, ist bekannt, dass gesunde Probanden unter diesen Bedingungen Primingeffekte zeigen. (Maljkovic & Nakayama, 1996; Geyer et al., 2007). In Studie 1 untersuchten wir die Auswirkungen von offener und verdeckter Aufmerksamkeitsablenkung bei Gesunden. In Studie 2 und 3 untersuchten wir die Auswirkungen offener (Studie 2) und verdeckter (Studie 3) Aufmerksamkeitsablenkung auf Positionsprimingeffekte in rechtshemispherischen Patienten mit und ohne Beteiligung des Parietallappens und kontrastierten die Ergebnisse gegen die Vorhersagen des Modells von Pisella und Mattingley (2004).

Studie 1: Positionspriming überdauert offene und verdeckte Ablenkung von Aufmerksamkeit bei Gesunden

In Studie 1 zeigten wir, dass Positionsprimingeffekte auch nach offener und verdeckter Aufmerksamkeitsverschiebung in einem Priming of pop-out-Paradigma bei gesunden Probanden auftreten. Um zu testen, ob offene Aufmerksamkeitsverschiebung und damit verbundene Augenbewegungen einen Einfluss haben würden, erfassten wir Primigeffekte jeweils nach Sakkaden vom linken und ins vom linken ins rechts visuelle Feld in zwei getrennten Experimenten jeweils an retinotop identischen und spatiotop identischen Positionen.

Die Probanden zeigten Primingeffekte, Erleicherung und Hemmung nach Sakkaden, sowohl in retinotopen als auch in spatiotopen Koordinaten.

Das Ausmaß der Erleicherung in den beiden Experimenten war vergleichbar sowohl zwischen den Experimenten, als auch vergleichbar mit der Erleicherung, die wir in einer Kontrollbedingung ohne Sakkaden zwischen den Durchgängen erhalten hatten. Der Hemmungseffekt, den wir auf retinotop identischen Positionen erhalten hatten, war größenmäßig vergleichbar mit dem Hemmungseffekt, den wir auf spatiotop identischen Positionen erhalten hatten, jedoch von geringerem Ausmaß als der Hemmungseffekt, den wir in dem Kontrollexperiment erhalten hatten. Der unterschiedliche Einfluss von offener Aufmerksamkeitsablenkung auf Erleicherungs- und Hemmungseffekt zum einen und zum anderen speziell die Verringerung der Größe des Hemmungseffektes passt zu der Annahme, dass zum einen Erleichterung und Hemmung zwei verschiedene – die visuelle Suche unterstützende – Mechanismen widerspiegeln und zum anderen, dass der Hemmungseffekt der weniger robuste Effekte und der von mehr Faktoren beeinflussbare von beiden zu sein scheint (Maljkovic & Nakayama, 1996; Geyer et al., 2007; Geyer & Müller, submitted).

Um den Einfluss von verdeckter Aufmerksamkeitsablenkung zu testen, wurde – wiederum in zwei verschiedenen Experimenten – die Aufmerksamkeit der Probanden zwischen den Durchgängen abgelenkt, während sie die Fixation in der Mitte des Bildschirmes aufrechterhielten. Aufmerksamkeitsablenkungen können entweder unwillkürlich durch das Auftauchen irrelevanterReize auftreten (exogen) oder willkürlich durch freiwilliges Hinwenden der Aufmerksamkeit zu (z.B. verhaltensrelevanten) Reizen (endogen) erfolgen (Müller & Rabbitt, 1989). Dementsprechend wurden Primingeffekte nach exogener und nach endogener Ablenkung separat erfasst und mit Effekten aus einem Kontrollexperiment ohne Aufmerksamkeitsablenkung verglichen.

Sowohl Erleicherung als auch Hemmung waren sowohl miteinander als auch über alle Experimente hinweg miteinander im Hinblick auf ihre Größe vergleichbar.

Studie 1 zeigte, dass Primingeffekte bei gesunden Probanden trotz offener und verdeckter Aufmerksamkeitsablenkung vorhanden sind. Das Vorhandensein der

Primingeffekte lässt auf eine intakte raum-zeitliche Integration schließen. Generell lässt sich vermuten, dass diese Effekte wichtige Mechanismen reflektieren.

Das Resultat der Experimente zum Einfluss der offenen Aufmerksamkeitsablenkung stützen – desweiteren - die Annahme, dass Erleichterung und Hemmung zwei unterschiedliche Mechanismen der visuellen Suche widerspiegeln. Der Vergleich der Resultate (v.a. das Ergebnis im Hinblick auf den Hemmungseffekt) aus den Experimenten zur offenen und verdeckten Aufmerksamkeit lässt darauf schließen, dass die Effekte offene Aufmerksamkeitsablenkung auf einem anderen Weg überdauern als verdeckte Aufmerksamkeitsverschiebungen.

Studie 2: Zeigen Patienten mit rechtsparietalen Läsionen räumliche Remapping-Defizite nach Sakkaden?

Das Ziel von Studie 2 war, die Annahme zu überprüfen, ob der parietale Cortex ein mögliches neuronales Korrelat für räumliche Remapping-Mechanismen darstellt. Wir analysierten Primingeffekte nach offener Aufmerksamkeitsverschiebung an retinotop („Sakkadenexperiment“) und spatiotop („Räumliches Remapping Experiment“) identischen Positionen und in einem Kontrollexperiment ohne Aufmerksamkeitsverschiebung in einer Gruppe gesunder Probanden, einer Gruppe rechtshemipshärischer Patienten ohne und einer Gruppe rechtshemisphärischer Patienten mit parietaler Beteiligung. Durch die separate Erfassung von Priming auf retiotop identischen und spatiotop identischen Positionen hatten wir die Gelegenheit, den reinen Einfluss von Sakkaden ohne Remapping auf retinotop identischen und den Einfluss von Remapping - induziert durch sakkadenbedingte Verschiebung - der räumlichen Stimulusanordnung zu entflechten. Dies erschien wichtig, nachdem in vielen Experimenten (z. B. Duhamel et al., 1992a; Heide et al., 1995) Sakkaden- und Remappingeinfluss miteinander konfundiert waren.

Wir fanden Erleicherung und Hemmung in allen Gruppen im Kontrolleperiment ohne Aufmerksamkeitsverschiebung, wobei der Effekt der Erleicherung in der Gruppe der parietalen Patienten sogar noch stärker ausgeprägt war. Desweiteren fanden wir Erleicherung und Hemmung in allen Gruppen gleichermaßen ausgeprägt im „Sakkadenexperiment“, d.h. nach Sakkaden, jedoch der Stimuluanordnung an retinotop identischen Positionen. Im „Räumlichen Remapping Experiment“ zeigten sowohl Gesunde als auch Patienten ohne parietale Beteiligung Erleicherung und Hemmung. Patienten mit rechts parietalen Schädigungen allerdings, zeigten weder Erleicherung noch Hemmung. Unsere Ergebnisse stehen im Einklang mit Befunden bei gesunden Probanden (siehe auch die Experimente in Studie 1), die IOR (ein Effekt, der ebenfalls als visuelle Suchleistungen unterstützend angesehen wird) nach Sakkadendurchführung sowohl in retinotop als auch spatiotop identischen Koordinaten zeigten (Sapir et al., 2004). Und mit Befunden bei Patienten mit parietalen Schädigungen, die in der gleichen Studie von Sapir et al., (2004) IOR nach Sakkadenausführung in retinotopen, jedoch nicht in spatiotopen Koordinaten zeigten.

Unsere Ergebnisse sprechen dafür, dass der parietale Kortex an der Durchführung von räumlichem Remapping beteiligt ist. Desweiteren unterstützen sie die Annahme, dass räumliche Remapping-Defizite zu visuellen Suchdefiziten bei Patienten mit parietalen Schädigungen beitragen. Nicht vorhandene Erleicherung könnten z.B. zur Erklärung der Ergebnisse einer Studie von Shimozaki et al., (2003) beitragen, die zeigte, dass Patienten mit parietalen Läsionen (im Gegensatz zu Gesunden, die zielgerichtete Sakkaden hin zum Zielreiz durchführten) zufällige Blickbewegungen - statt zielgerichtete Sakkaden zu einem Zielreiz - in einem Suchdisplay durchführten, obwohl sie den Ort des zu suchenden Zielreizes bereits in einem Vorschaudisplay gesehen hatten. Das Fehlen von Hemmung in der visuellen Suche hingegen, könnte zur Erklärung des Phänomens des Wiederholten Absuchens von bereits abgesuchten Stellen bei Patienten mit parietalen Läsionen (Pisella et al., 2004) beitragen.

Studie 3: Induziert verdeckte Aufmerksamkeitsablenkung räumliche Remapping-Anforderungen? Hinweise aus der Untersuchung von Patienten mit rechts parietalen Läsionen

Das Ziel von Studie 3 war es, die Annahme des Modells zu testen, dass verdeckte Aufmerksamkeitsverschiebungen räumliche Remapping-Anforderungen induzieren. Das hier verwendete Paradigma ließ insbesondere zu, die Auswirkungen von verdeckter Aufmerksamkeitsverschiebung ohne Konfundierung einer räumlichen Verschiebung des Suchdisplays (wie z.B. in der Studie von Vasquez & Danckert, 2008 gegeben), zu untersuchen. Folglich konnten wir insbesondere die Annahme von Pisella und Mattingley (2004) überprüfen, nach der Aktivitäten auf der Salienzkarte nach verdeckter Aufmerksamkeitsablenkung aufgefrischt und nicht (wie nach offener Aufmerksamkeitsverschiebung) repositioniert werden. Nachdem wir aufgrund der Ergebnisse in Studie 2 annehmen konnten, dass räumliche Remapping-Defizite bei Patienten mit rechts parietalen Läsionen auftreten, konnten wir aus der Leistung dieser Patienten Schlüsse auf die Intaktheit oder auf mögliche Defizite bei der raum-zeitlichen Integration nach verdeckter Aufmerksamkeitsverschiebung ziehen. Dazu verglichen wir abermals Primingeffekte bei Gesunden und Patienten mit rechts-hemisphärischen Läsionen mit und ohne parietale Beteiligung in drei Experimenten in einem Kontrollexperiment ohne und in zwei Experimenten mit verdeckter Aufmerksamkeitsverschiebung (jeweils exo- und endogen). Das „Kontrollexperiment“ in Studie 3 hatte im Vergleich zum „Kontrollexperiment“ in Studie 2 ein sehr langes Interstimulusintervall (2100 ms vs. 1000 ms). Obwohl alle Gruppen in dem „Kontrollexperiment“ in Studie 3 ebenfalls signfikante Erleicherung und Hemmung zeigten, war der Hemmungseffekt bei Patienten mit parietalen Schädigungen signifikant reduziert Hemmungeffekt im Vergleich zu Patienten ohne parietale Schädigung und gesunden Probanden. Der Befund der reduzierten Hemmung in dem „Kontrollexperiment“ mit langem ereignislosem Interstimulusintervall konnte trat wohl eher

aufgrund des Verfalls dieser (im Vergleich zu Erleicherung anfälligeren und zeitlich nicht so sehr überdauernden; Maljkovic & Nakayama, 1996) Komponente einhergehend mit einem oftmals mit parietalen Schädigungen assoziiertem Aufmerksamkeitsdefizit (z. B. Pardo et al., 1991) auf, als aufgrund eines Problems in der raum-zeitlichen Integration von aufeinanderfolgender visueller Information. Wenn dem so sei, konnte man erwarten, dass – vorausgesetzt die Annahme, dass verdeckte Aufmerksamkeitsverschiebung würde nicht durch das Verschwinden von Primingeffekten unterstützt werden – eine derartige Reduktion von Inhibition in der Gruppe der Patieten mit parietalen Schädigungen nicht mehr auftreten würde, wenn Ereignisse (d.h. periphere Ablenker) innerhalb des langen Interstimulusintervalls auftreten. Tatsächlich waren in den Ergebnissen im „nichtrelevanten Ablenker-“ (11) und im „relevanten Ablenkerexperiment“ (12) keine Unterschiede zwischen den Gruppen zu finden. Lateralsierte Modifizierungen in den Reaktionszeiten in beiden Experimenten zeigten sich in allen Gruppen gleichermaßen und konnten deswegen auf den Einfluss der peripheren Ablenker und der dadurch hervorgerufenen Aufmerksamkeitsablenkung zurückgeführt werden. Da sich diese Einflüsse in allen Gruppen und nicht spezifisch in der Gruppe der parietalen Patienten zeigten, gab es keinerlei Hinweise auf eine spezifische Beeinträchtigung von raum-zeitlicher Integrationsleistung aufgrund von Remapping-Defiziten nach verdeckter Aufmerksamkeitsablenkung. Da jedoch von einem derartigen räumlichen Defizit in diesen Patienten ausgegangen werden kann (siehe auch die Ergebnisse in Studie 2), gehen unsere Ergebnisse nicht mit der Annahme des Modells von Pisella und Mattingley (2004) konform, das verdeckte Aufmerksamkeitsverschiebungen räumliche Remappinganforderungen induzieren und dass diese von Remapping-Mechanismen, die im Parielalcortex angesiedelt sind, erfüllt werden.

Ausblick

In den hier vorgestellten Studien haben wir ein Positionspriming-Paradigma als Methode zur Erfassung raum-zeitlicher Integrationsleistungen etabliert. Den theoretischen Hintergrund für die Untersuchungen lieferte das Model zum räumlichen Remapping von Pisella und Mattingley (2004).

Die Kombination aus praktikabler Methode und fruchtbarem Modell im Hinblick auf die Überprüfung weiterer Hypothesen lässt auf zukünftige Studien hoffen, die sich Fragen wie z.B. der Auswirkung von links parietalen Läsionen auf Priming nach offener und verdeckter Aufmerksamkeitsablenkung oder der Auswirkung von richtungsspezifischen Sakkaden im jeweils ipsi- und contralläsionalem visuellen Feld bei Patienten mit links vs. rechts parietalen Schädigungen widmen.

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Curriculum vitae

Leandra Bucher

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Education and research experience

since 2005	Doctoral student and research assistant at the chair of "General and Experimental psychology" (Ludwig Maximilian University Munich, Germany)
	"Spatio-temporal integration in visual search in patients with fronto-parietal lesions" (DFG funded project)
2005	Degree (diploma) in Psychology (University Eichstaett-Ingolstadt, Germany)
	"Optokinetische Stimulation bei Neglect in der Frührehaphase - eine Therapiestudie –" (diploma thesis)
2002 – 2003	Studies on language processing using lateralized readiness potentials (student helper, University Eichstaett-Ingolstadt, Germany)
1998	Paralegal (lawyer´s office Brüninghaus, Kolbermoor, and commercial vocational school, Traunstein, Germany)
1995	Abitur (Finsterwalder Gymnasium, Rosenheim, Germany)

Erklärung

Hiermit erkläre ich, Leandra Bucher, geb. am 26.09.1976, dass ich die vorliegende Dissertation mit dem Titel „Spatial remapping mechanisms and their impairments in patients with right parietal lesions“ ohne fremde Hilfe angefertigt und nur die angegebenen Quellen als Hilfsmittel verwendet habe.

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Leandra Bucher