Dynamic Upper and Lower Visual Field Preferences Within the Human Dorsal Frontoparietal Attention Network

Antje Kraft,^{1#} Wieland H. Sommer,^{1,2,3#} Sein Schmidt,^{1,2}
and Stephan A. Brandt^{1,2*}

¹Department of Neurology, Charité, Berlin Neuroimaging Center, Berlin, Germany

²Bernstein Center for Computational Neuroscience Berlin, Berlin, Germany

³Department of Clinical Radiology, University Hospital-Grosshadern,
Ludwig-Maximilians University, Munich, Germany

Abstract: Both in nonhuman primates and in humans, behavioral differences between the upper and lower visual field have been identified in distinct subprocesses of attention. Advantages of the lower field have been explained by its higher spatial resolution; those of the upper field by its higher efficiency in attentional shifting. The physiological basis of visual field asymmetries within the frontoparietal attention network (FPN) remains unclear. This study investigates the physiological correlates of upper and lower field preferences within the FPN using event-related functional magnetic resonance imaging. The paradigm separated two attentional subprocesses during a visual search task. Whether in the upper or lower field, the attention of subjects was first directed at stationary locations (spatial orienting) and then shifted between locations to search for a target (visual search) in easy or difficult search displays. Depending on the task phase (spatial orienting vs. easy visual search), upper and lower visual field preferences in the FPN changed. The analysis revealed a lower field preference during stationary spatial orienting and an upper field preference during visual search. We conclude that also higher areas represent upper and lower visual field asymmetries depending on distinct subcomponents of visuospatial attentional processing. *Hum Brain Mapp* 32:1036–1049, 2011. © 2010 Wiley-Liss, Inc.

Key words: endogenous attention; fMRI; topographic mapping; visual attention; visual search

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[#]These authors contributed equally to this work.

*Correspondence to: Prof. Stephan A. Brandt, Department of Neurology, Universitätsmedizin Charité, Charitéplatz 1, Berlin 10117, Germany. E-mail: stephan.brandt@charite.de

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INTRODUCTION

Over the past 20 years, several studies have documented differences in the processing of visual information in the upper and lower visual fields [see Danckert and Goodale, 2003 for a review]. Most tasks resulted in a behavioral advantage in the lower visual field. This becomes apparent in measures such as faster reaction times or enhanced accuracy rates [Ellison and Walsh, 2000; He et al., 1996; Kraft et al., 2005, 2007; Malinowski et al., 2007; Previc, 1990]. Levine and McAnany [2005], however, analyzed behavioral advantages of the upper and lower field and found them to be dependent on the class of stimuli. A lower field advantage was found for stimuli which differ in contrast, hue and motion. In contradistinction, stimuli differing in

the apparent distance from the observer revealed an advantage for the upper visual field. The results were interpreted in an evolutionary context: most tasks requiring the differentiation of small movements, contrast or hue take place in the lower visual field, while approaching dangers are mostly located in the upper visual field. This may have led to the specialization of the upper and lower visual field for distinct class of stimuli or tasks, respectively [Levine and McAnany, 2005].

Alternative theories associated the behavioral upper and lower field differences with differences in attentional processing rather than perceptual asymmetries [Danckert and Goodale, 2003; Previc, 1990]. In particular, it is suggested that the lower field advantage can be explained with a finer-grained attentional resolution within the lower field [He et al., 1996]. Evidence was obtained in several behavioral studies [He et al., 1996; Intriligator and Cavanagh, 2001; Kraft et al., 2005, 2007]. For instance, in two of our previous studies, we found a lower field advantage for an endogenous spatial orienting task in which the focus of attention had to be voluntarily directed at separate or adjacent locations in the upper or lower visual field. The upper visual field condition revealed higher error rates, while reaction times were similar for both visual fields [Kraft et al., 2005]. The same lower field advantage was confirmed in a second endogenous spatial orienting task performed to quantify the influence of distractor position, task difficulty and visual field position [Kraft et al., 2007].

Although most attentional paradigms revealed lower visual field advantages, others revealed no differences between the fields [Carrasco et al., 2001]. Some even measured an advantage for the upper visual field [Fecteau et al., 2000]. The behavior in attentional tasks therefore seems to be more complex. A thorough review of the relevant literature was published by Danckert and Goodale [2003]. The authors concluded that an advantage of the lower visual field is revealed by tasks using stationary attention or skilled movements of the hand, like pointing or grasping, while shifts of the attentional focus were more efficient and faster within the upper visual field. Similar findings were described by Previc [1990] and were also interpreted in evolutionary terms: The author proposed that the visual field is divided into peripersonal space (close to the body) and extrapersonal space (beyond reaching distance). The former corresponds approximately to the lower visual field, while the latter is represented by the upper visual field. Everyday needs have led to a specialization of the lower visual field for goal directed actions, while the upper visual field is specialized for visual search or large scale scene perception [Previc, 1990]. Therefore, the upper and lower visual fields show attentional biases which have evolved quite differently.

Physiological evidence for a lower visual field preference has already been found on the level of the retina. There is a greater density of ganglion cells in the superior retina, which receives information from the lower visual

field. This asymmetry was described in the order of 60% [Curcio et al., 1987].

Further evidence for lower field preferences can be attributed to the level of the lateral geniculate nucleus and extrastriate visual areas. In the lateral geniculate nucleus, evidence for an upper and lower field asymmetry was obtained in monkeys [Schein and de Monasterio, 1987]. Rubin et al. showed that the perception of illusory contours is significantly better in the lower visual field. This asymmetry indicates a neural specialization in extrastriate visual areas and therefore suggests additional cortical levels of asymmetric processing of the upper and lower visual field [Rubin et al., 1996].

Cortical correlates of asymmetries in visual areas and subregions of the frontoparietal attention network (FPN) are only poorly understood. A greater representation of the lower visual field was reported in monkey studies for higher visual areas V6A and MT (middle temporal) [Galletti et al., 1999; Maunsell and Van Essen, 1987].

In the human brain, a dorsal and ventral attention network was identified in several functional neuroimaging studies (functional magnetic resonance imaging, [fMRI]) involved in bottom-up and top-down processes of attention [see Corbetta et al., 2008 for a review]. Bottom-up processes (stimulus-driven attention) are associated with activations of the ventral network [see also Hahn et al., 2006]. In contradistinction, the dorsal FPN, including parietal subregions along the intraparietal sulcus (IPS), as well as frontal regions (e.g. the frontal eye field [FEF]), is suggested to be involved in top-down-controlled attentional processes. Thereby, a bilateral FPN is activated in different attentional subprocesses such as shifting, maintenance, and visual search [e.g. Kelley et al., 2008; Muller et al., 2003b] with an extensive overlap of regions activated in distinct subprocesses of attention. It was also observed that endogenous and exogenous attention activated the same regions of the human brain but led to rather different lateralizations. Tasks with a predominating endogenous component of attention tended rather towards a left hemispheric lateralization [Corbetta et al., 2000; Hopfinger et al., 2000; Nobre et al., 1997], while tasks involving rather exogenous attention showed stronger activation within the right hemisphere [Hahn et al., 2006; Kim et al., 1999]. This indicates that lateralization effects could result both from specificities in endogenous and exogenous attention, as well as visual field representations, i.e. if attention is directed to one side of the vertical meridian (left or right visual field) or to both sides (upper or lower visual field) [Corbetta et al., 2002]. A series of visual search studies revealed that subregions of the posterior parietal cortex (PPC) and the FEF are involved in visual selection mechanisms of search [Donner et al., 2000, 2002; Muller et al., 2003b]. A differential modulation for search difficulty was revealed in subregions anterior intraparietal sulcus (AIPS) and intraparietal junction with the transverse occipital sulcus (IPTO) [Donner et al., 2003].

Some neuroimaging studies addressed how the visual field is represented in subregions of the FPN in humans

[Hagler and Sereno, 2006; Saygin and Sereno, 2008; Schluppeck et al., 2005; Silver et al., 2005; Tootell et al., 1996, 1998]. Areas of the PPC and the FEF are known to have representations of both the upper and the lower visual field. Several studies identified spatial topographies in areas V7, IPS1, IPS2, or the FEF [Hagler and Sereno, 2006; Saygin and Sereno, 2008; Schluppeck et al., 2005; Silver et al., 2005]. However, no neuroimaging study directly compared upper or lower field activations for differential perceptual or attentional subprocesses within these regions.

In a previous study, we examined the spatial coding of the left and right hemifield along the dorsal FPN during two distinct subprocesses of attention with fMRI [Sommer et al., 2008]. In a visual search task a cueing and search period were separately analyzed, representing spatial orienting and search, respectively. We observed that the spatial coding for the left and right hemifields, as well as the hemispheric lateralization of activation changed depending on the attentional subcomponent: During spatial orienting, the left hemisphere had a preference for the contralateral right visual field, while the right hemisphere processed both hemifields equally. Activation was stronger lateralized into the left hemisphere. In contrast, during visual search, the pattern of contralateral preference and lateralization was inversed. Our results therefore demonstrated the dynamic nature of spatial coding and lateralization of activation; both were dependent on the type of attentional subprocess.

Thus, we hypothesize that visual field preferences within subregions of the FPN are not stable, but rather change according to the subprocess of visual attention. A change from a lower field preference for tasks in which attention is stationary to an upper field preference for tasks involving shifts of attention could provide a physiological correlate for the model described by Danckert and Goodale [2003], which proposes differences in visual field preferences due to attentional parameters.

The aim of this study is to investigate with event-related fMRI, if the areas of the FPN show lower and upper visual field preferences for stationary spatial attention and shifting (visual search), respectively [Danckert and Goodale, 2003; Previc, 1990]. In particular, we test the hypothesis that the asymmetries dynamically change, depending on different subprocesses of attention (i.e., spatial orienting vs. visual search). During spatial orienting, the attentional focus is directed to a location and then remains stationary. We suggest that predominantly top-down driven endogenous attention is involved in this subprocess. In contrast, during visual search, both endogenous and exogenous attention processes are suggested to be involved in order to find the target [Wolfe et al., 2003]. While difficult search tasks certainly require both endogenous and exogenous attention, as the attentional focus has to be actively shifted among a search array, easy search tasks may lead to a pop-out effect where attention is predominantly stimulus-driven or exogenous [Wolfe et al., 2003].

We tested both subprocesses of spatial attention in the same task and in the same group of subjects, since the comparability of results in attention tasks is strongly affected by different experimental paradigms or settings. This allows a direct comparison of asymmetries without being biased by inter-subject variability or variability between different experimental settings. Using this approach, we show that subregions of the FPN show dynamic upper and lower visual field preferences depending on specific subcomponents of visuospatial attention.

MATERIALS AND METHODS

Subjects

Twenty-five subjects participated in the experiments. Participants were students from the Humboldt-University and were paid for participation. They all had normal vision, were strictly right-handed (according to the Edinburgh handedness questionnaire [Oldfield, 1971]), and had no known neurological or visual disorders. Written, informed consent was obtained from all subjects. Our study was conducted in conformity with the Declaration of Helsinki and was approved by the ethics committee of the Charité.

Analyzing covert attention processes, it is important to make sure that subjects can perform the task without overt eye movements. Each subject was tested in a behavioral experiment (240 trials) on the ability to perform the task covertly. To ensure that subjects maintained proper fixation, eye movements were recorded with the I-View-System (50 Hz) of SMI (Sensomotoric Instruments, Berlin-Teltow) applying the I-View 3.01.11 software. Eye data were analyzed with ILAB software [Gitelman, 2002]. The criteria for participating in the fMRI experiment were an error rate of less than 10% and eye movements in less than 5% of all trials. Eleven of the participating subjects (mean age = 25.3 years; SD = 2.3 years) fulfilled the criteria and were tested in the fMRI experiment. All of them were also participated in our previous fMRI study [Sommer et al., 2008].

Experimental Paradigm

We applied an event-related fMRI paradigm to investigate upper and lower visual field effects during distinct attention subprocesses of a visual search task [see also Sommer et al., 2008]. The paradigm included the subprocesses spatial orienting and visual search (see Fig. 1). During spatial orienting (SO) the focus of attention remains stationary at voluntarily attended positions [Collie et al., 2000; Nakayama and Mackeben, 1989]. During visual search (VS), the focus shifts through the visual field [Wolfe, 2003].

The paradigm consisted of a circular array of 7° visual angle in radius, comprising 12 equidistant placeholders.

Figure 1.

Visual search paradigm separating spatial orienting (SO) and visual search (VS). After a fixation period, a central cue was pointed at the relevant visual field (upper or lower) for the next trial. When stimuli appeared, subjects had to search covertly for a target line among the 6 positions of the cued visual field. Task difficulty was manipulated by the number of distractors with non-vertical orientations in the relevant visual field (easy: 2; difficult: 5).

Subjects were instructed to maintain central fixation throughout the whole experiment. The paradigm distinguished between (i) the cueing period (spatial orienting), where subjects attend covertly either to six positions within the upper or lower visual field and (ii) a target period (visual search), where subjects covertly search for a target line at the six positions within the cued visual field under easy or difficult search demands, respectively.

The SO period started when the upper or lower part of the fixation symbol turned white (see Fig. 1). A variable delay of 3, 6, or 9 s was utilized to prevent anticipatory responses [Muller et al., 2003a, b]. The placeholders allowed subjects to more precisely direct voluntary attention within the cued visual field [Kraft et al., 2005, 2007; Turatto et al., 2000].

The spatial orienting was followed by the VS phase, in which 12 black lines of 1° visual angle with different orientations replaced the placeholders and a target line had to be detected among distractors within the previously cued visual field. The target line had an angle of 30° counterclockwise to the horizontal meridian, while the distractor lines had angles of 60°, 90°, 120°, and 150°, respectively (see Fig. 1).

During the VS period, task difficulty was modified by the number of lines within the relevant visual field which had an orientation other than a vertical one [Forster and Ward, 1991]. There were two difficulty levels in our search phase: in the easy search condition only two lines were nonvertical within the cued visual field. In the difficult search condition, five of the six lines within the cued visual field had an orientation other than a vertical one (see

Fig. 1). In both, easy and difficult search conditions the six positions of the noncued visual field were filled with the same pattern of lines throughout all trials. Equal numbers of easy and difficult trials were used and the target was absent in 50% of all trials.

Subjects responded with an absent/present judgment as accurately and quickly as possible by pressing buttons with their right index or right middle finger (randomized across subjects).

Within two sessions, of 6 runs each, each visual field was cued 120 times (24 trials with 3 s cueing interval, 48 trials with 6 or 9 s cueing interval, respectively). The two sessions for each subject were acquired on the same day with a sufficient delay between them. The duration of one run was 12 min and 54 s. This was composed of 40 trials with three different intertrial-intervals (ITIs) plus an additional fixation phase in the beginning and end of each run. The ITI was 15 s (20% of trials), 18 s (40%), or 21 s (40%), depending on the duration of the cue (3, 6, or 9 s). Data from the 3 s cueing interval were only introduced to ensure that subjects paid attention during the whole cueing period. They were not further analyzed because of the delay in the blood oxygen level dependent (BOLD) response [Muller et al., 2003a].

Data Acquisition

At first, a high quality anatomical three-dimensional data set was acquired in a Siemens 1.5 Tesla Scanner using a T1-weighted sagittal Flash sequence (TR/TE = 38/5 ms, FA = 30°, voxel size = 1 mm³). Two acquisitions were used for excellent gray-white contrast for accurate segmentation and reconstruction of individual surface structures.

fMRI data were acquired in a 3 Tesla GE Scanner using an 8-channel-phased array coil. A screen was mounted in front of a standard head coil, on which stimuli were displayed by a LCD projector and a custom-made lens. Subjects viewed the screen through a mirror located above their eyes. To minimize head movements and to stabilize the subject's head, we used a vacuum cushion inside the coil. BOLD signals were measured with a high resolution echo planar imaging (EPI) sequence, covering the whole brain (voxel size 2 × 2 × 3.5 mm³, TR = 3 s, TE = 60 ms, FA = 90°, 32 slices, 128 × 128 matrix). Each fMRI run contained three preliminary saturation scans for T1 equilibration effects. After three runs, a 3D-SPGR anatomical scan, consisting of 222 slices, was recorded to align the functional data on the previously recorded high-quality anatomical images.

Data Analysis

We used BrainVoyager QX (BrainInnovation, Maastricht, Netherlands) to analyze the fMRI data. All anatomical and functional data were individually registered into a 3D-

stereotactic coordinate system [Talairach and Tournoux, 1988]. Functional volumes in all the sessions for each subject were preprocessed including slice time correction, linear trend removal, motion correction, and high pass filtering of frequencies above three cycles per time course to remove slow drifts in fMRI signal. All runs with motion exceeding 2 mm were excluded. Data from one subject was completely excluded from analysis due to excessive motion artifacts.

A segmentation of white and gray matter was performed from the high resolution anatomical MRI images of each subject and surfaces of the white matter were reconstructed. As described in previous experiments, four ROIs of the dorsal FPN were predefined by anatomical criteria [see Beauchamp et al., 2001; Donner et al., 2000, 2002; Muller et al., 2003b; Paus, 1996], as these areas have been identified as the core components of the FPN in previous fMRI studies [see Corbetta and Shulman, 2002 for review]: IPTO, AIPS, posterior intraparietal sulcus (PIPS), and FEF. Specifically, the horizontal branch of the IPS was subdivided into AIPS and PIPS at the transition from its posterior deep segment and its anterior less deep, and extensively truncated, segment. IPTO was placed posterior and ventral to PIPS, at the junction of the IPS with the transverse occipital sulcus. The FEF ROI was placed at the intersection of the precentral sulcus with the superior frontal sulcus according to Beauchamp et al. [2001]. Talairach coordinates are listed in Table I. Functional data were then realigned onto the high resolution T1-Flash images by using the anatomical information of the 3D-SPGR anatomical scans.

After z-transformation, general linear models (GLM) were used to compute statistical maps. The model contained an idealized reference function as predictor of the effect of interest. This reference function was generated by convolving a model of the hemodynamic impulse response (a γ function with $\delta = 2.5$ and $\tau = 1.25$) with a square-wave function representing the experimental protocol [Boynton et al., 1996]. The regressors SO-upper-3s, SO-lower-3s, SO-upper-6s, SO-lower-6s, SO-upper-9s, SO-lower-9s, easy-VS-upper, easy-VS-lower, difficult-VS-upper and difficult-VS-lower were included in the statistical model. The analysis was performed both for the group data, and for single subjects' data using the surface-based statistic analysis tools of Brainvoyager QX, including the conversion of voxels in 1 mm^3 iso-voxel. In single subjects, regions activated by SO (SO vs. fixation) or VS (VS vs. fixation) were separately identified ($P < 10^{-5}$, uncorrected). For the group analysis, regions activated by SO and VS were identified using a whole brain volume random effects analysis (RFX, $P < 0.005$, corrected). These activations were marked on the surface of a single subject separately for SO and VS (cluster threshold of 50 mm^2 on the surface). It is important to note that the activated voxels were defined across both upper and lower field conditions. With the whole brain random effects analysis, we also determined regions sensitive to all experimental conditions

TABLE I. Talairach coordinates

ROI	Left Hemisphere			Right Hemisphere		
	<i>x</i>	<i>y</i>	<i>z</i>	<i>x</i>	<i>y</i>	<i>z</i>
IPTO	-27 ± 3	-74 ± 5	21 ± 4	27 ± 4	-72 ± 6	26 ± 7
PIPS	-19 ± 3	-63 ± 6	40 ± 6	24 ± 5	-62 ± 8	40 ± 5
AIPS	-31 ± 6	-55 ± 8	43 ± 7	29 ± 6	-53 ± 8	44 ± 3
FEF	-28 ± 4	-8 ± 4	48 ± 3	31 ± 6	-6 ± 3	48 ± 4

Table 1 shows the mean *x*, *y*, *z* Talairach coordinates, and standard deviation ($\pm$ SD) of region-of-interest (ROI) in the frontoparietal network. Abbreviations: FEF, frontal eye field; AIPS, anterior intraparietal sulcus; PIPS, posterior intraparietal sulcus; IPTO, intraparietal sulcus junction with the transverse occipital sulcus.

(SO, easy VS and difficult VS), i.e., the conjunction [Nichols et al., 2005; Price and Friston, 1997].

Both, in single subjects' and group analysis, for each activated voxel ($1 \text{ voxel} = 1 \text{ mm}^3$) that corresponded to the activation on the surface (range from -1 to 3 mm), a *t*-test was performed separately for SO and VS, calculating whether the voxel responded more strongly to the upper or the lower visual field. These *t*-tests were based on the beta values of the voxel during the upper or lower visual field condition, respectively. The resulting *t*-values indicated a preference either for the upper visual field (positive *t*-values) or for the lower visual field (negative *t*-values). *T*-values were color coded on the cortical surface. Green and red color indicated a preference for the upper visual field and for the lower visual field, respectively. White color was used for *t*-values around zero, indicating that the voxel is activated by the subprocess of visuospatial attention, but does not have a significant preference for either visual field.

Further statistical data analyses were conducted with the SPSS software (Version 16.0). Based on the individual anatomical predefined ROIs, for each subject a histogram of *t*-values for each ROI was calculated. Then, for each subject a percent value of voxels showing a significant preference (i.e., *t*-value significantly different from 0) to the upper or lower visual field, respectively, was calculated for each individual ROI (IPTO, PIPS, AIPS, FEF) in each hemisphere (left, right) for each phase (SO, easy VS, difficult VS). Percentage values were entered in one four-way repeated measures analysis of variance (ANOVAs) with factors phase (SO, easy VS, difficult VS), hemisphere (left, right), area (IPTO, PIPS, AIPS, FEF), and visual field bias (upper, lower), as well as three separate four-way repeated measures ANOVAs with factors phase (SO and easy VS; SO and difficult VS; easy VS and difficult VS, respectively), hemisphere (left, right), area (IPTO, PIPS, AIPS, FEF), and visual field bias (lower, upper). If necessary, degrees of freedom and *P*-values were corrected by the Greenhouse-Geisser formula.

Since the spatial orienting phase did not require a separate response, we could only obtain behavioral results for

TABLE II. Summary of behavioral results

Condition	RT (ms)	ER (%)	d'	c
Upper hemifield	1,221 ± 66	6.01 ± 1.58	3.40 ± 0.25	0.21 ± 0.08
Lower hemifield	1,170 ± 53	7.21 ± 1.19	3.07 ± 0.18	0.28 ± 0.06
Easy search	1,060 ± 55	3.93 ± 0.98	3.66 ± 0.18	0.21 ± 0.06
Difficult search	1,341 ± 66	9.28 ± 1.90	2.92 ± 0.23	0.27 ± 0.08
Easy upper hemifield	1,078 ± 62	4.18 ± 1.30	3.45 ± 0.20	0.19 ± 0.07
Easy lower hemifield	1,042 ± 49	3.68 ± 0.94	3.48 ± 0.15	0.23 ± 0.07
Difficult upper hemifield	1,370 ± 74	7.84 ± 1.99	2.97 ± 0.24	0.22 ± 0.09
Difficult lower hemifield	1,309 ± 61	10.73 ± 1.97	2.66 ± 0.22	0.32 ± 0.10

Reaction times (RT), error rates (ER), target detection sensitivity (d'), and the response criterion (c) for visual search in the upper and lower visual field, comparison of easy and difficult search conditions and comparison of the behavioral data of the upper and lower visual field during easy and difficult search conditions. Data shown ± standard errors.

the visual search conditions. To obtain behavioral results, we calculated mean RTs and accuracy rate differences (percentage of error, d' as a measure of target detection sensitivity and the criterion (c) as a measure of the response tendency [MacMillan and Creelman, 2004].

All behavioral measures were separately calculated for easy and difficult VS in the upper and lower visual field, respectively. Mean RTs and accuracy rates were entered in a multivariate and separate univariate two-way ANOVAs with factors visual field (upper vs. lower) and task difficulty (easy vs. difficult). Detection sensitivity and response criterion were entered in two-way ANOVAs with factors visual field and task difficulty. Stimulus onset asynchronies (different lengths of the cue phase) were not entered as a separate factor, because they did not contain the same number of trials; rather, the 3 s cue condition was less frequent. Where appropriate, degrees of freedom and P -values were corrected (Greenhouse-Geisser) and Bonferroni-corrected pairwise comparisons were then used to evaluate the difference between specific condition means.

RESULTS

Behavioral Results

A multivariate ANOVA for RTs and error rates with factors “visual field” (upper vs. lower visual field) and “task difficulty” (easy vs. difficult search) was calculated (see Table II). Analysis did not achieve a significant main effect for the factor “visual field” [$F(2,8) = 4.08$; $P > 0.05$]. However, the main effect for the factor “task difficulty” reaches significance [$F(2,8) = 36.81$; $P < 0.001$], reflecting that subjects respond faster and more accurately in the easy than in the difficult task. Also the interaction between “visual field” and “task difficulty” was significant [$F(2,8) = 8.41$; $P < 0.05$]. Table II illustrates that subjects respond slightly faster and accurate in the lower than the upper visual field in the easy task. In the difficult task, there is a trend towards better accuracy but longer RT in the upper than the lower visual field, suggesting a speed-accuracy trade-off. However, univariate analyses of RTs and error rates

revealed no significant interactions between “visual field” and “task difficulty” and none of the relevant post hoc comparisons between the upper and lower visual field showed a significant difference.

Separate univariate two-way ANOVAs with factors “task difficulty” and “visual field” were also calculated for d' and c , respectively (see Table II). A significant main effect was found for the factor “task difficulty” for d' [$F(1,9) = 18.48$; $P < 0.005$] but not for c [$F(1,9) = 0.56$; $P > 0.05$]. Both measures did not achieve a significant main effect for the factor “visual field”; d' [$F(1,9) = 2.09$; $P > 0.05$] and c [$F(1,9) = 1.15$; $P > 0.05$]. There were no significant interactions between those two factors (d' [$F(1,9) = 1.55$; $P > 0.05$]; c [$F(1,9) = 0.23$; $P > 0.05$]). As in previous visual search studies [Zenger and Fahle, 1997] the response criterion showed positive values in all experimental conditions, i.e., the frequency of missed targets was higher than the frequency of false alarms. This “no-tendency” is a known phenomenon in visual search tasks. More important, there was no significant criterion shift between visual search in the upper or the lower visual field or between easy and difficult search. Careful analysis of target detection sensitivity only revealed a significant uncorrected post hoc comparison between the upper and lower visual field, with higher detection sensitivity in the upper than in the lower visual field ($P = 0.039$).

fMRI Results

Results of the group analysis for the experimental conditions SO, easy VS, and difficult VS are illustrated in Figure 2 (marked on the surface of a single subject). Activations of the FPN were observed for all three experimental conditions; similar to our previous studies [Donner et al., 2000, 2002; Muller et al., 2003b]. However, activation patterns for subprocesses SO, easy VS and difficult VS vary inside the regions of the FPN, as well as in their extent of visual field preference (see Figs. 2–4).

To get an overall measure of changes in visual field preferences between distinct attentional conditions, mean t -values for the entire dorsal FPN of both hemispheres

Figure 2.

Visual field preferences of activated voxels during spatial orienting (SO) and visual search (VS) visualized in the group data. Group data were marked on the surface of a single subject separately for SO, easy and difficult VS; the figure displays the dorsal posterior view of the inflated left and right hemispheres with representation of t -values on the surfaces. The preference for the upper or lower visual field was determined by t -tests for all voxels activated by SO and easy/difficult VS ($P < 0.005$, RFX, cluster threshold: 50 mm²). Negative (red) and positive (green) t -values indicate a preference for the lower and upper visual

field, respectively. Voxels with t -values < -2.26 or > 2.26 show a significant visual field preference ($P < 0.05$) and are indicated by dark red or green, respectively. White color indicates voxels involved in the process with no preference for either visual field. Abbreviations: FEF, frontal eye field; CeS, central sulcus; AIPS, anterior intraparietal sulcus; PIPS, posterior intraparietal sulcus; IPTO, intraparietal sulcus junction with the transverse occipital sulcus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

were separately calculated for SO, easy and difficult search, respectively. During SO, we found the most negative mean t -values ($T: -1.06$), corresponding to a stronger preference of the lower visual field. Difficult search led to mean t -values around zero ($T: 0.01$), while easy search showed the highest mean t -values ($T: 0.59$), corresponding to a stronger preference for the upper visual field (see also Supporting Information Fig. 1 for a detailed analysis of t -values in areas IPTO, PIPS, AIPS, and FEF, as well as for two control ROIs visual occipital [VO] and the motor cortex [MC]).

To evaluate a potential visual field effect, a four way repeated measures ANOVA with factors task phase (SO, easy VS, difficult VS), hemisphere (left, right), area (IPTO, PIPS, AIPS, FEF) and visual field bias (upper, lower) was conducted. Significant main effects for the factors task [$F(2,18) = 10.17$, $P < 0.001$] and area [$F(1,7,15) = 10.08$, $P < 0.01$], as well as a significant two-way interaction between the factor task and area [$F(2,4,22) = 10.38$, $P < 0.001$] were obtained, reflecting that a higher percentage of voxels showed a visual field preference during SO in area IPTO than in PIPS, AIPS or FEF: Post hoc comparisons revealed significant differences between IPTO and PIPS ($P < 0.05$), IPTO and AIPS ($P < 0.01$) and IPTO and the FEF ($P < 0.01$) for SO, but not for easy or difficult VS (all $P >$

0.05). For SO, PIPS also showed a significantly higher percentage of voxels with a visual field preference than area AIPS ($P < 0.05$). This was not obtained for easy or difficult VS conditions (all $P > 0.05$).

More important, a significant two-way interaction between the factors task and visual field bias [$F(2,18) = 3.87$, $P < 0.05$] was obtained. No significant main effects were revealed for the factors hemisphere [$F(1,9) = 0.01$, $P > 0.05$] and visual field bias [$F(1,9) = 1.28$, $P > 0.05$]. Nor did the interactions between the factors task and hemisphere [$F(2,18) = 0.25$, $P > 0.05$], hemisphere and area [$F(1,4,12.6) = 0.61$, $P > 0.05$], hemisphere and visual field bias [$F(1,9) = 2.26$, $P > 0.05$], area and visual field bias [$F(3,27) = 0.59$, $P > 0.05$] reach significance. Also no significant three- or four-way interaction revealed significance (task $\times$ hemisphere $\times$ area [$F(2.5,22.4) = 0.34$, $P > 0.05$]; task $\times$ hemisphere $\times$ bias [$F(2,18) = 1.04$, $P > 0.05$]; task $\times$ area $\times$ bias [$F(2.7,24.4) = 1.43$, $P > 0.05$]; hemisphere $\times$ area $\times$ bias [$F(3,27) = 1.34$, $P > 0.05$]; task $\times$ hemisphere $\times$ area $\times$ bias [$F(6,54) = 1.22$, $P > 0.05$]).

As the two-way interaction between task and visual field bias revealed significance, three separate four-way repeated measures ANOVAs were conducted—again with the factor task phase (SO and easy VS; SO and difficult VS; easy VS and difficult VS, respectively), hemisphere,

Figure 3.

Visual field preferences of activated voxels during spatial orienting (SO) and easy visual search (VS) visualized in the group data on the basis of individual anatomical ROIs of $N = 10$ subjects. Histograms depict mean percentage of voxel t -values within predefined ROIs of the dorsal FPN. The range of t -values represented by each bar is 1.13. Voxels with t -values < -2.26 or > 2.26 show a significant visual field preference ($P < 0.05$). The

standard error of the mean is indicated for each bar. The color conventions for visual field preferences are described in Figure 2. Abbreviations: FEF, frontal eye field; AIPS, anterior intraparietal sulcus; PIPS, posterior intraparietal sulcus; IPTO, intraparietal sulcus junction with the transverse occipital sulcus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

area and visual field bias—to test how the three experimental conditions differ in visual field preferences.

The four-way ANOVA on the upper and lower activation differences between SO and easy VS revealed a significant main effects for the factors task phase [$F(1,9) = 30.33$, $P < 0.0001$] and area [$F(1.3,12.1) = 15.73$, $P < 0.001$]. The main effects for the factors hemisphere [$F(1,9) = 0.05$, $P > 0.05$] and visual field preference [$F(1,9) = 0.01$, $P > 0.05$] were not significant. However, analysis revealed significant two-way interactions for the factors task phase and area [$F(1.2,11) = 17.16$, $P < 0.001$], as well as for the factors

task phase and visual field preference [$F(1,9) = 16.02$, $P < 0.01$], indicating a change in visual field preference from a lower field advantage in SO, as compared with an upper field advantage during easy VS (see Fig. 3). Post hoc comparisons reflect that significantly more voxels showed a lower visual field bias during SO than during easy VS ($P < 0.001$). For easy VS significantly more voxels had a preference for the upper visual field than for the lower visual field ($P < 0.05$). For SO, the difference between voxels showing an upper or lower visual field bias revealed no significance ($P > 0.05$). All other interactions were not

Figure 4.

Visual field preferences of activated voxels during spatial orienting (SO) and visual search (VS) visualized in two single subjects. Dorsal posterior view of the inflated right hemispheres of two subjects (S1 left, S9 right) with representation of *t*-values on the surface. The preference for the upper or lower visual field was determined by *t*-tests for all voxels activated by SO and VS (*P*-values indicated below surfaces). The color convention for visual

field preferences is described in Figure 2. Abbreviations: FEF, frontal eye field; AIPS, anterior intraparietal sulcus; PIPS, posterior intraparietal sulcus; IPTO, intraparietal sulcus junction with the transverse occipital sulcus. Yellow dotted lines: predefined individual anatomical ROIs. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

significant (task $\times$ hemisphere [$F(1,9) = 0.24, P > 0.05$]; hemisphere $\times$ area [$F(1.2,11.2) = 0.1, P > 0.05$]; hemisphere $\times$ bias [$F(1,9) = 3.32, P > 0.05$]; area $\times$ bias [$F(3,27) = 0.35, P > 0.05$]; task $\times$ hemisphere $\times$ area [$F(3,27) = 0.01, P > 0.05$]; task $\times$ hemisphere $\times$ bias [$F(1,9) = 0.72, P > 0.05$]; task $\times$ area $\times$ bias [$F(1.7,9) = 1.68, P > 0.05$]; hemisphere $\times$ area $\times$ bias [$F(3,27) = 0.89, P > 0.05$]; task $\times$ hemisphere $\times$ area $\times$ bias [$F(3,27) = 1.44, P > 0.05$]).

In contradistinction, the four-way ANOVA on the upper and lower activation differences between SO and difficult VS revealed no significant main effect for the factor task phase [$F(1,9) = 5.02, P > 0.05$]. Only the main effect for the factor area [$F(1.5,13.6) = 10.76, P < 0.001$], and the two-way interaction between task phase and area were significant [$F(3,27) = 10.81, P < 0.0001$]. The interactions between the factors task phase and visual field preference [$F(1,9) = 2.96, P > 0.05$], as well as between task phase, area and visual field preference reached no significance [$F(3,27) = 1.26, P > 0.05$], thus indicating no change in visual field preference for SO, as compared with difficult VS. The main effects for the factors hemisphere [$F(1,9) = 0.05, P > 0.05$] and visual field preference [$F(1,9) = 0.09, P > 0.05$] were not significant. No further interaction reaches significance (task $\times$

hemisphere [$F(1,9) = 0.002, P > 0.05$]; hemisphere $\times$ area [$F(1.5,13.3) = 0.58, P > 0.05$], hemisphere $\times$ bias [$F(1,9) = 1.88, P > 0.05$]; area $\times$ bias [$F(3,27) = 1.03, P > 0.05$]; task $\times$ hemisphere $\times$ area [$F(3,27) = 0.35, P > 0.05$]; task $\times$ hemisphere $\times$ bias [$F(1,9) = 1.39, P > 0.05$]; hemisphere $\times$ area $\times$ bias [$F(1.3,11.9) = 1.59, P > 0.05$]; task $\times$ hemisphere $\times$ area $\times$ bias [$F(3,27) = 1.2, P > 0.05$]).

The four way-ANOVA on the upper and lower activation differences between easy and difficult VS revealed only a significant main effect for the factor visual field bias [$F(1,9) = 7.54, P < 0.05$], indicating that significantly more voxels show a significant bias to the upper visual field than the lower visual field during both, easy and difficult VS. This is in accordance with the slightly higher detection sensitivity during VS in the upper as compared with the lower visual field (but note that subjects were numerically slower and less accurate in the upper visual field during the easy task, though these differences were not significant). All other main effects (task [$F(1,9) = 3.64, P > 0.05$]; hemisphere [$F(1,9) = 0.35, P > 0.05$]; area [$F(1.4,12.8) = 0.11, P > 0.05$]) and interactions reached no significance ([task $\times$ hemisphere [$F(1,9) = 0.8, P > 0.05$]; task $\times$ area [$F(3,27) = 0.31, P > 0.05$]; hemisphere $\times$ area [$F(3,27) = 1.57, P > 0.05$]; task $\times$ bias [$F(1,9) = 0.12, P > 0.05$];

hemisphere $\times$ bias [$F(1,9) = 0.02, P > 0.05$]; area $\times$ bias [$F(3,27) = 0.9, P > 0.05$]; task $\times$ hemisphere $\times$ area [$F(1.5,13.1) = 1.12, P > 0.05$]; task $\times$ hemisphere $\times$ bias [$F(1,9) = 0.66, P > 0.05$]; task $\times$ area $\times$ bias [$F(1.3,11.8) = 1.47, P > 0.05$]; hemisphere $\times$ area $\times$ bias [$F(3,27) = 1.22, P > 0.05$]; task $\times$ hemisphere $\times$ area $\times$ bias [$F(3,27) = 0.96, P > 0.05$]).

Several regions in the FPN were activated by SO, easy VS and difficult search (see Fig. 2). The conjunction analysis revealed that 21.6% of these voxels showed a lower visual field preference during SO, whereas only 5.6% showed an upper visual field preference during easy VS. We found that 4.6% of conjunction voxels change their field preference directly from a significant lower visual field preference during SO to a significant upper visual field preference during easy VS. The region of these voxels was located in the right PIPS at the border to IPTO (Talairach coordinates $24 \pm 2, -66 \pm 2, 37 \pm 2$). The direct reversal in visual field preference is also evident in subregions of the FPN of single subjects. Figure 4 illustrates the right hemispheres of two subjects (S1 and S9) during SO and VS. Patches of cortex, for instance at the border of PIPS and IPTO, showed a lower field bias during SO which changes to a substantial upper field bias during VS.

DISCUSSION

We found that visual preferences in the dorsal FPN differ for attentional subprocesses, with a preference for the lower visual field during stationary spatial orienting (SO) and a preference for the upper visual field during search (VS). This reversal was more apparent during easy search rather than difficult search.

The dynamic changes in visual field preference for SO and VS are in accordance with our previous results, where left and right hemifield preferences were analyzed in the same group of subjects [Sommer et al., 2008]. Minimizing the inter-experiment variability in that way, it can be shown that similar subregions inside the ROIs of the FPN were activated during SO and VS in both experiments. Only the visual field preferences change dynamically depending on the respective subprocess. However, stimuli were always presented over both the upper and the lower visual field. Therefore the differences do not result from varying sensory stimulation between the visual fields, but rather reflect spatial attention mechanisms [Niemeier et al., 2005].

Upper and Lower Visual Field Preferences

This study only allowed us to analyze a behavioral correlate of upper and lower field preferences during the VS period. On the other hand the fMRI results reflect a disparity in lower and upper visual field preference in the FPN during SO and VS, respectively. This is in line with previous behavioral studies analyzing visual field advantages in distinct attention tasks. Studies analyzing behavioral performances in stationary voluntary attention found

stable lower field advantages [He et al., 1996; Intriligator and Cavanagh, 2001; Kraft et al., 2005, 2007]. In contrast, measuring behavioral performances during visual search in the upper or lower visual fields revealed evidence for an upper visual field advantage [Fecteau et al., 2000; Previc, 1990, 1998], which is in line with our present finding of a slightly higher detection sensitivity in the upper visual field condition. This finding matches with the fact that significantly more voxels in the FPN showed a significant bias to the upper visual field than the lower visual field during both easy and difficult VS (see Fig. 4). However, we found the strongest bias to the upper visual field during the easy search task (see Fig. 3), and no behavioral difference between the upper and lower visual field during easy visual search. In the difficult task, there is a trend towards better accuracy but longer RT in the upper than the lower visual field, suggesting a speed-accuracy trade-off.

In general, visual field advantages for the upper or lower visual field are a matter of controversy. On the one hand previous behavioral experiments suggested that the dynamic of the attentional focus plays an important role. Danckert and Goodale [2003] and Previc [1990, 1998] proposed that a lower field advantage exists for stationary attention, while shifts of the attentional focus are more precisely handled in the upper visual field. Alternative explanations for upper and lower field advantages are being discussed: As described in the introduction, there are several parameters which were processed more precisely in the upper visual field [Levine and McAnany, 2005]. This was especially the case when distractors were located both in the upper and lower visual field, as in the present experiment. Alternatively the advantage of the upper visual field during VS could also result from the fact that the attentional focus can be more easily divided within the upper visual field [Malinowski et al., 2007].

However, not all attention tasks resulted in behavioral differences between the upper and lower visual field: Michael and Ojeda [2005] found no behavioral differences between the upper and lower visual field in a visual search task. Because of an eccentricity of 2.3° , targets were located marginal to the fovea. Thus, as proposed by Danckert and Goodale [2003], large scale shifts of the attentional focus involving the dorsal FPN network (action pathway) might not be necessary. Instead, the task could be processed mainly by the ventral perception pathway, which deals primarily with foveal vision.

Carrasco and Frieder [1997] also performed visual search tasks in which an upper visual field advantage cannot be observed. A discrimination tasks with a visual search component even resulted in an advantage for the lower visual field [Carrasco et al., 2001]. In this experiment, behavioral results were recorded for eight positions in a circular array. The positions were arranged like the points of a compass (N, E, S, W, NE, SE, SW and NW). Interestingly the advantage of the lower visual field resulted nearly exclusively from poor behavioral results on the position N, while positions NE, SE, SW, and NW did

not show significant behavioral differences. This argues against a general disadvantage of the upper visual field and for a specific disadvantage of the position N, located in the upper visual field on the vertical meridian [see also Liu et al., 2006 for a physiological correlate of the vertical meridian asymmetry]. None of the twelve positions in our experiment were located on the horizontal or vertical meridian. It is thus unlikely that the disadvantage of the position N has any effect in our experiment. Furthermore, the experiment of Carrasco et al. [2001] included a grating discrimination task, which requires a finer grained resolution than that required in our experiment, which, again, favours the argument for a lower visual field advantage [Danckert and Goodale, 2003; Intriligator and Cavanagh, 2001].

In summary, it becomes obvious that behavioral visual field advantages are not a fixed constant but rather depend on subprocesses of attention, number and scale of attentional shifts, and type of targets. Nevertheless, this study complements the numerous behavioral studies by exploring the cortical correlates of visual field advantages. Since we were able to show the concomitant preference change within the frontoparietal network, our data confirm a cortical basis of visual field preferences. This supports models suggested by several other authors [Danckert and Goodale, 2003; Previc, 1990].

It is important to note that spatial and nonspatial attentional functions are processed in the same subregions of the FPN [Coull and Frith, 1998; Donner et al., 2000; Muller et al., 2003b]. In line with this assumption a large part of voxels inside the subregions of the FPN was equally activated for both visual fields. We found differences in the number of voxels showing a bias for the upper or lower visual field, with a higher number of voxels in area IPTO as compared all other areas of the FPN, especially during the period of spatial orienting. This is in line with the fact that area IPTO has a precise topographical organization [Silver et al., 2005]. Even so, the bias for the lower and upper visual search during spatial orienting and visual search (especially easy VS) was evident within all areas of the FPN. The conjunction analysis indicates that most notably different regions inside the FPN show a preference for the lower or upper visual field during SO or VS respectively. A direct change in visual field preference for the period of SO and easy VS can only be observed in the right PIPS at the border to IPTO.

The focus of our study was the analysis of the dorsal visuo-attentional processing stream. Recent findings suggest that ventral visual areas did not show upper or lower visual field preferences [Large et al., 2008]. In this study, no evidence was obtained for a visual field bias in VO areas. However, we cannot differentiate between single visual areas, as we did not perform localizer tasks to map the visual areas (V1, V2, V3/VP, V4v, or LO (lateral occipital)).

The comparison of SO and VS in the current study could be biased by the fact that SO consisted of the presentation of a visual cue and did not require any explicit

motor response. In contrast, VS required a motor response. To what extent this may influence visual field preferences and lateralization effects within the dorsal FPN [see also Sommer et al., 2008] is an open question. Up to now, no influences of the response hand side on the pattern of visual field preferences have been reported in the literature [Hagler and Sereno, 2006; Previc, 1990; Silver et al., 2005].

An alternative explanation could be that SO and VS differed in the direction of attentional shifts. While SO involved up-down shifts, VS also required left-right shifts. Thus, the different patterns of visual field preference could partly originate from the different directions of attentional shifts. As discussed in Sommer et al. [2008], previous experiments demonstrated that activation within the dorsal FPN depend more on the hemifield in which the attentional focus is located than on its direction [Corbetta et al., 1993]. Additionally, Macaluso and Patria [2007] recently showed that the axis of orientation of attentional shifts does not produce different brain activations.

Endogenous Versus Exogenous Attention and Search Difficulty Manipulations?

As stated above, previous models [Danckert and Goodale, 2003] suggested differences in visual field preference due to attentional parameters, with a specialization of the lower visual field during stationary visual-attentional discrimination and a specialization of the upper visual field in the fast and exact shifting of attention.

In this study, the reversal between lower and upper visual field preferences between SO and VS is initially in accordance with this idea. The amount of shifting, however, should be higher in our difficult search condition than in our easy search condition. One would therefore expect a stronger upper field advantage in difficult search than in easy search. But in our data, the reverse pattern is evident.

Looking at the proposed models of upper and lower field advantages in more detail, Danckert and Goodale [2003] reveal that these models did not specify whether shifts of attention should be stimulus-driven (exogenous, reflexive) or top-down-driven (endogenous, voluntary) in order to reveal an upper field advantage. As also stated in [Sommer et al., 2008], SO and VS might not only differ in terms of the dynamics of the attentional focus, with mainly stationary attention in SO and shifting in VS. It is plausible that both subprocesses differ with respect to the endogenous and exogenous attention dimension [Collie et al., 2000; Nakayama and Mackeben, 1989; Weichselgartner and Sperling, 1987]. Considering this dimension may help to explain our findings with respect to upper and lower visual field preferences in SO, easy and difficult search: During spatial orienting, the attentional focus is directed to a location and then remains stationary. We suggest that predominantly top-down-driven endogenous attention is involved in this subprocess [Kraft et al., 2005, 2007]. In contrast, during search, both endogenous and

exogenous attention processes could be necessary for finding the target. In the easy search condition, endogenous attention might not be necessary because the target can pop out, thus causing a predominantly stimulus-driven or exogenous shift of attention. In contradistinction, the difficult search condition certainly involved a high amount of endogenous orienting, as targets had to be examined more serially [Wolfe et al., 2003].

Thus, the change in visual field preference between SO and VS could be directly related to the amount of endogenous and exogenous attention with a lower visual field preference during mainly endogenously driven spatial orienting and an upper visual field preference during mainly exogenously-driven easy visual search. In contrast, difficult search with a combination of both revealed no clear visual field preference. A similar gradual change in visual field preferences in dependence of the amount of endogenous or exogenous attention has already been described in our previous experiment, which analyzed the spatial coding of the left and right visual field during SO and VS [Sommer et al., 2008].

Following this reasoning, the proposed models [Danckert and Goodale, 2003; Previc, 1990] could only be applied for exogenous attention shifts within the upper visual field. Further research is necessary to verify these aspects. It is well accepted that, depending on the type of cue (peripheral vs. central) single exogenous or endogenous shifts can be induced experimentally [Nakayama and Mackeben, 1989; Collie et al., 2000]. A two factorial design with factors visual field (upper vs. lower visual field) and type of attentional shift (exogenous vs. endogenous) has the potential to test whether upper and lower field preferences in the FPN depend on the type of attention.

CONCLUSION

Visual field preferences within subregions of the frontoparietal network are not stable, but rather change according to the subprocess of visual attention. Initially, the change from a lower to an upper visual field preference for spatial orienting and visual search, respectively, could provide a physiological correlate for existing models, which specifically suggested differences in visual field preference due to attentional parameters [Danckert and Goodale, 2003]. The specialization of the lower visual field (peripersonal space) for visual-attentional discrimination could be reflected by the preference for the lower visual field during spatial orienting (stationary endogenous attention). The specialization of the upper visual field in the fast and exact shifting of attention would correlate with the preference for the upper visual field during visual search. However, task difficulty manipulations in the present experiment indicate that the upper field advantage in shifting could depend rather on the type of shift (exogenous vs. endogenous) than the number of shifts. Our results support the notion that exogenous attention leads

to an upper field preference of the frontoparietal network, while this preference is reversed during endogenous attention. Further research is necessary to clarify this aspect.

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REFERENCES

- Beauchamp MS, Petit L, Ellmore TM, Ingelholm J, Haxby JV (2001): A parametric fMRI study of overt and covert shifts of visuospatial attention. *Neuroimage* 14:310–321.
- Boynton GM, Engel SA, Glover GH, Heeger DJ (1996): Linear systems analysis of functional magnetic resonance imaging in human V1. *J Neurosci* 16:4207–4221.
- Carrasco M, Frieder KS (1997): Cortical magnification neutralizes the eccentricity effect in visual search. *Vis Res* 37:63–82.
- Carrasco M, Talgar CP, Cameron EL (2001): Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spat Vis* 15:61–75.
- Collie A, Maruff P, Yucel M, Danckert J, Currie J (2000): Spatio-temporal distribution of facilitation and inhibition of return arising from the reflexive orienting of covert attention. *J Exp Psychol Hum Percept Perform* 26:1733–1745.
- Corbetta M, Shulman GL (2002): Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3: 201–215.
- Corbetta M, Kincade JM, Shulman GL (2002): Neural systems for visual orienting and their relationships to spatial working memory. *J Cogn Neurosci* 14:508–523.
- Corbetta M, Miezin FM, Shulman GL, Petersen SE (1993): A PET study of visuospatial attention. *J Neurosci* 13:1202–1226.
- Corbetta M, Kincade JM, Ollinger JM, McAvooy MP, Shulman GL (2000): Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat Neurosci* 3:292–297.
- Corbetta M, Patel G, Shulman GL (2008): The reorienting system of the human brain: From environment to theory of mind. *Neuron* 58:306–324.
- Coull JT, Frith CD (1998): Differential activation of right superior parietal cortex and intraparietal sulcus by spatial and nonspatial attention. *Neuroimage* 8:176–187.
- Curcio CA, Sloan KR Jr, Packer O, Hendrickson AE, Kalina RE (1987): Distribution of cones in human and monkey retina: individual variability and radial asymmetry. *Science* 236:579–582.
- Danckert JA, Goodale MA (2003): Ups and downs in the visual control of actions. In: Johnson-Frey SH editor. *Taking Action: Cognitive Neuroscience Perspectives on Intentional Actions*. Cambridge, MA: MIT Press. pp 29–64.
- Donner T, Kettermann A, Diesch E, Ostendorf F, Villringer A, Brandt SA (2000): Involvement of the human frontal eye field and multiple parietal areas in covert visual selection during conjunction search. *Eur J Neurosci* 12:3407–3414.

- Donner TH, Kettermann A, Diesch E, Ostendorf F, Villringer A, Brandt SA (2002): Visual feature and conjunction searches of equal difficulty engage only partially overlapping frontoparietal networks. *Neuroimage* 15:16–25.
- Donner TH, Kettermann A, Diesch A, Villringer A, Brandt SA (2003): Parietal activation during visual search in the absence of multiple distractors. *Neuroreport* 14:2257–2261.
- Ellison A, Walsh V (2000): Visual field asymmetries in attention and learning. *Spat Vis* 14:3–9.
- Fecteau JH, Enns JT, Kingstone A (2000): Competition-induced visual field differences in search. *Psychol Sci* 11:386–393.
- Forster DH, Ward PA (1991): Asymmetries in oriented-line detection indicate two orthogonal filters in early vision. *Proc R Soc Lond B Biol Sci* 243:75–81.
- Galletti C, Fattori P, Kutz DF, Gamberini M (1999): Brain location and visual topography of cortical area V6A in the macaque monkey. *Eur J Neurosci* 11:575–582.
- Gitelman DR (2002): ILAB: A program for postexperimental eye movement analysis. *Behav Res Methods Instrum Comput* 34:605–612.
- Hagler DJ Jr, Sereno MI (2006): Spatial maps in frontal and prefrontal cortex. *Neuroimage* 29:567–577.
- Hahn B, Ross TJ, Stein EA (2006): Neuroanatomical dissociation between bottom-up and top-down processes of visuospatial selective attention. *Neuroimage* 32:842–853.
- He S, Cavanagh P, Intriligator J (1996): Attentional resolution and the locus of visual awareness. *Nature* 383:334–337.
- Hopfinger JB, Buonocore MH, Mangun GR (2000): The neural mechanisms of top-down attentional control. *Nat Neurosci* 3:284–291.
- Intriligator J, Cavanagh P (2001): The spatial resolution of visual attention. *Cogn Psychol* 43:171–216.
- Kelley TA, Serences JT, Giesbrecht B, Yantis S (2008): Cortical mechanisms for shifting and holding visuospatial attention. *Cereb Cortex* 18:114–125.
- Kim YH, Gitelman DR, Nobre AC, Parrish TB, LaBar KS, Mesulam MM. (1999): The large-scale neural network for spatial attention displays multifunctional overlap but differential asymmetry. *Neuroimage* 9:269–277.
- Kraft A, Muller NG, Hagendorf H, Schira MM, Dick S, Fendrich RM, Brandt SA (2005): Interactions between task difficulty and hemispheric distribution of attended locations: implications for the splitting attention debate. *Brain Res Cogn Brain Res* 24:19–32.
- Kraft A, Pape N, Hagendorf H, Schmidt S, Naito A, Brandt SA (2007): What determines sustained visual attention? The impact of distracter positions, task difficulty and visual fields compared. *Brain Res* 1133:123–135.
- Large ME, Culham J, Kuchinad A, Aldcroft A, Vilis T (2008): fMRI reveals greater within- than between-hemifield integration in the human lateral occipital cortex. *Eur J Neurosci* 27:3299–3309.
- Levine MW, McAnany JJ (2005): The relative capabilities of the upper and lower visual hemifields. *Vis Res* 45:2820–2830.
- Liu T, Heeger DJ, Carrasco M (2006): Neural correlates of the visual vertical meridian asymmetry. *J Vis* 6:1294–1306.
- Macaluso E, Patria F (2007): Spatial re-orienting of visual attention along the horizontal or the vertical axis. *Exp Brain Res* 180:23–34.
- MacMillan NA, Creelman CD (2004): *Detection Theory: A User's Guide*. New Jersey: Lawrence Erlbaum Associates.
- Malinowski P, Fuchs S, Muller MM (2007): Sustained division of spatial attention to multiple locations within one hemifield. *Neurosci Lett* 414:65–70.
- Maunsell JH, Van Essen DC (1987): Topographic organization of the middle temporal visual area in the macaque monkey: Representational biases and the relationship to callosal connections and myeloarchitectonic boundaries. *J Comp Neurol* 266:535–555.
- Michael GA, Ojeda N (2005): Visual field asymmetries in selective attention: Evidence from a modified search paradigm. *Neurosci Lett* 388:65–70.
- Muller NG, Bartelt OA, Donner TH, Villringer A, Brandt SA (2003a) A physiological correlate of the “Zoom Lens” of visual attention. *J Neurosci* 23:3561–3565.
- Muller NG, Donner TH, Bartelt OA, Brandt SA, Villringer A, Kleinschmidt A (2003b) The functional neuroanatomy of visual conjunction search: A parametric fMRI study. *Neuroimage* 20:1578–1590.
- Nakayama K, Mackeben M (1989): Sustained and transient components of focal visual attention. *Vis Res* 29:1631–1647.
- Nichols T, Brett M, Andersson J, Wager T, Poline JB (2005): Valid conjunction inference with the minimum statistic. *Neuroimage* 25:653–660.
- Niemeier M, Goltz HC, Kuchinad A, Tweed DB, Vilis T (2005): A contralateral preference in the lateral occipital area: Sensory and attentional mechanisms. *Cereb Cortex* 15:325–331.
- Nobre AC, Sebestyen GN, Gitelman DR, Mesulam MM, Frackowiak RS, Frith CD (1997): Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* 120 (Part 3):515–533.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Paus T (1996): Location and function of the human frontal eye-field: A selective review. *Neuropsychologia* 34:475–483.
- Price CJ, Friston KJ (1997): Cognitive conjunction: a new approach to brain activation experiments. *Neuroimage* 5:261–270.
- Previc FH (1990): Functional specialisation in the lower and upper visual fields in humans: Its ecological implications. *Behav Brain Sci* 13:519–542.
- Previc FH (1998): The neuropsychology of 3-D space. *Psychol Bull* 124:123–164.
- Rubin N, Nakayama K, Shapley R (1996): Enhanced perception of illusory contours in the lower versus upper visual hemifields. *Science* 271:651–653.
- Saygin AP, Sereno MI (2008): Retinotopy and attention in human occipital, temporal, parietal, and frontal cortex. *Cereb Cortex* 18:2158–2168.
- Schein SJ, de Monasterio FM (1987): Mapping of retinal and geniculate neurons onto striate cortex of macaque. *J Neurosci* 7:996–1009.
- Schluppeck D, Glimcher P, Heeger DJ (2005): Topographic organization for delayed saccades in human posterior parietal cortex. *J Neurophysiol* 94:1372–1384.
- Silver MA, Ress D, Heeger DJ (2005): Topographic maps of visual spatial attention in human parietal cortex. *J Neurophysiol* 94:1358–1371.
- Sommer WH, Kraft A, Schmidt S, Olma MC, Brandt SA (2008): Dynamic spatial coding within the dorsal frontoparietal network during a visual search task. *PLoS ONE* 3:e3167.
- Talairach J, Tournoux P (1988): *Co-planar Stereotactic Atlas of the Human Brain*. New York: Thieme.

- Tootell RB, Dale AM, Sereno MI, Malach R (1996): New images from human visual cortex. *Trends Neurosci* 19:481–489.
- Tootell RB, Hadjikhani NK, Vanduffel W, Liu AK, Mendola JD, Sereno MI, Dale AM (1998): Functional analysis of primary visual cortex (V1) in humans. *Proc Natl Acad Sci USA* 95:811–817.
- Turatto M, Benso F, Facoetti A, Galfano G, Mascetti GG, Umiltà C (2000): Automatic and voluntary focusing of attention. *Percept Psychophys* 62:935–952.
- Weichselgartner E, Sperling G (1987): Dynamics of automatic and controlled visual attention. *Science* 238:778–780.
- Wolfe JM (2003): Moving towards solutions to some enduring controversies in visual search. *Trends Cogn Sci* 7:70–76.
- Wolfe JM, Butcher SJ, Lee C, Hyle M (2003): Changing your mind: On the contributions of top-down and bottom-up guidance in visual search for feature singletons. *J Exp Psychol Hum Percept Perform* 29:483–502.
- Zenger B, Fahle M (1997): Missed targets are more frequent than false alarms: A model for error rates in visual search. *J Exp Psychol Hum Percept Perform* 23:1783–1791.