Check for updates

Selective Visual Dimension Weighting Deficit after Left Lateral Frontopolar Lesions

S. Pollmann[1], K. Mahn[2], B. Reimann[3], R. Weidner[4], M. Tittgemeyer[5], C. Preul[5], H. J. Müller[2], and D. Y. von Cramon[5,6]

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/365/1962329/jocn.2007.19.3.365.pdf by guest on 18 May 2021

Abstract

■ The left lateral frontopolar (LFP) cortex showed dimension change-related activation in previous event-related functional magnetic resonance imaging studies of visual singleton feature search with non-brain-lesioned participants. Here, we tested the hypothesis that LFP actively supports changes of attention from the old to the new target-defining dimension in singleton feature search. Singleton detection was selectively slowed in this task when the target-defining dimension changed in patients with left LFP lesions, compared with patients with frontomedian lesions as well as with matched controls without brain lesions. We discuss a potential role of LFP in change detection when the optimal allocation of dimension-based attention is not clearly defined by the task. ■

INTRODUCTION

In functional magnetic resonance imaging (fMRI) experiments with non-brain-injured participants (Weidner, Pollmann, Müller, & von Cramon, 2002; Pollmann, Weidner, Müller, & von Cramon, 2000), we have found left lateral frontopolar (LFP) activation to be associated with cross-trial changes in the target-defining dimension in a visual singleton search task. Behavioral experiments using the same paradigm suggest that dimension changes (e.g., from a color-defined to a motion-defined target), but not feature changes within a dimension (e.g., from a red to a blue color-defined target), trigger a shift of attentional resources, or ''weight'' (cf. Duncan & Humphreys, 1989), from the old to the new target dimension (Found & Müller, 1996; Müller, Heller, & Ziegler, 1995). Potential target-defining dimensions (i.e., dimensions in which the target might differ from nontargets) are assigned weight in accordance with their instructed importance and variability across trials. Target detection requires that the target-defining dimension is weighted sufficiently to amplify the saliency signal generated within this dimension above the detection threshold. Dimension changes incur a cost because attentional weight must be shifted from the old to the new dimension. This notion was recently confirmed by the observation that, in singleton feature search, visual input areas for color and motion processing exhibit increased activation for cross-trial epochs of targets defined within the color and the motion dimension, respectively (Pollmann, Weidner, Müller, & von Cramon, 2006).

Whereas Pollmann et al. (2000) found left LFP activation to be associated with stimulus-driven dimension changes in singleton feature search (where the target differs from the nontargets in a single feature), Weidner et al. (2002, Experiment 1) found top-down-controlled dimension changes in singleton conjunction search (where the target differs from the nontargets in a conjunction of features) to be associated with increased activation in pregenual paracingulate cortex. In Experiment 2 of Weidner et al., participants performed both the singleton feature search task, in which dimension changes were stimulus-driven, and the singleton conjunction search task, in which dimension changes were top-down-controlled in a single fMRI session. Confirming the previous data, a double dissociation was observed with the LFP cortex showing a signal increase with stimulus-driven, but not top-down-controlled dimension changes, and pregenual frontomedian (FM) cortex exhibiting a signal increase with top-down-controlled, but not stimulus-driven dimension changes.

We postulated that the left LFP is involved in the control of stimulus-driven and FM cortex in top-down-controlled attentional weight shifts across visual dimensions (for a more detailed discussion, see the works of Pollmann, 2001, 2004). Functional activation, however, does not necessarily imply that these areas actively facilitate attention shifts across visual dimensions. Instead, frontopolar activation may reflect some process, such as monitoring or surprise, which accompanies dimension

[1]University of Magdeburg, [2]University of Munich, [3]University of Technology, Dresden, [4]Research Center Jülich, [5]University of Leipzig, [6]Max-Planck-Institute for Human Cognitive and Brain Sciences

© 2007 Massachusetts Institute of Technology

changes without directly contributing to visual dimension weighting. However, if the left frontopolar cortex supports a process that is necessary for the shifting of attentional resources from the old to the new target-defining dimension in singleton feature search, a lesion in this area should give rise to increased dimension change costs.

Involvement of the left LFP in stimulus-driven attention changes in an efficient visual search task such as that used in our fMRI studies was initially unexpected, as this area is thought to be involved in more complex tasks requiring the integration of multiple cognitive processes (see Ramnani & Owen, 2004, for a recent review). Moreover, frontopolar activation is not routinely observed in studies of visual attention shifts. Shifts of visuospatial attention have not usually been associated with frontopolar activation (e.g., Pollmann & Morrillo, 2003; Yantis et al., 2002; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001; Gitelman et al., 1999; Corbetta et al., 1998). However, left frontopolar activation was found to be increased on trials with invalid, relative to valid, exogenous (peripheral) cues in a spatial cueing paradigm (Lepsien & Pollmann, 2002). Likewise, frontopolar activation has not been consistently observed in studies of featural attention changes (e.g., Liu, Slotnick, Serences, & Yantis, 2003). Although Büchel et al. (1998) found a left LFP activation related to attention to motion (see their Figure 1), they did not discuss it, presumably because it failed to exceed their significance criterion. For endogenous motion cueing, an anterior cingulate activation was reported (Luks & Simpson, 2004), near the location of our pregenual anterior cingulate cortex activation for top-down-controlled visual dimension changes (Weidner et al., 2002). However, many studies of featural attention selectively imaged posterior brain areas (Culham, Cavanagh, Kanwisher, Dale, & Tootell, 1998; Beauchamp, Cox, & DeYoe, 1997), which limits the database relating to prefrontal contributions to featural attention. Thus, from these studies, no clear picture emerges as to the role of anterior prefrontal areas in the allocation of attention to features or dimensions.

On this background, the present study was designed to investigate whether the left LFP contributes actively to attention shifts between visual dimensions or whether the frontopolar activation reflects some process that accompanies visual dimension changes without actively facilitating attention shifts. To answer this question, we examined the performance of patients with left LFP lesions in visual singleton search. If the left frontopolar cortex facilitates the shift of attentional resources from the old to the new target-defining dimension in singleton feature search, a lesion in this area should slow down this attentional weight shifting, leading to increased search times on trials on which the target-defining dimension changes relative to the preceding trial, compared with trials on which the critical dimension remains the same. Attentional modulation of visual input areas in the occipito-temporal cortex was not the focus of this study, but was investigated in imaging studies using the same general paradigm (Pollmann et al., 2000, 2006).

Here, we tested a group of patients with left frontopolar lesions in a cross-dimensional singleton feature search paradigm. Based on our fMRI findings, we predicted that lesions of the left LFP, but not FM lesions, would lead to increased dimension change costs in singleton feature search.[1] These costs were predicted to be specific to changes between visual dimensions, that is, they were not expected to be observed for changes of feature values within a repeated visual dimension.

METHODS

Patients

We tested former patients of the Day Clinic of Cognitive Neurology of the University of Leipzig. Patients were selected from a database of 660 former patients. Selection criterion was an anterior prefrontal lesion that overlapped with or bordered either the dimension change-related left LFP activation focus obtained in non-brain-damaged participants in singleton feature search (Weidner et al., 2002; Experiment 2) or the dimension change-related pregenual FM activation focus obtained in singleton conjunction search in the same experiment. Patients with lesions overlapping with both foci were excluded. Written informed consent was obtained following the guidelines of the Max-Planck-Institute for Human Cognitive and Brain Sciences, Leipzig. The former patients and the normal control participants were paid for their participation. A description of the patient sample is given in Table 1. Each patient subgroup (lateral, medial) had its own age- and sex-matched non-brain-lesioned control group.

Individual lesions (Figure 1A) were manually segmented on the transverse slice of the MR images. All images were spatially coregistered to correct for position, orientation, image dimension, and head size to generate lesion density maps of the lateral and the medial lesion group (Figure 2).

The LFP group consisted of four patients who had lesions that overlapped with or bordered the LFP activation focus, at the lateral bank of the intermediate sulcus, in a previous fMRI experiment with normal participants (Weidner et al., 2002, Experiment 2). The lesions that bordered the activation maximum disconnected this area from the lateral posterior parts of prefrontal cortex. The FM group consisted of seven patients who had lesions that overlapped with the FM activation focus. Figure 3 presents a lesion density map in which, for each voxel, the percentage of patients with a lesion in the FM group is subtracted from the percentage of patients with a lesion in the LFP group. Within the left anterior prefrontal cortex, there was a clear demarcation between areas in which the percent-

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/365/1962379/jocn.2007.19.3.365.pdf by guest on 18 May 2021

Table 1. Patient Descriptions

Patient	*Sex*	*Age (Years)*	*Etiology*	*Lesion Sites*	*Accessory Lesions*
LFP group					
197	Female	59	AcoA aneurysm (ruptured): perioperative and postoperative (vasospastic) lesions	Left lateral frontal and lateral orbitofrontal (lateral orbital and posterior orbital gyrus lesioned); FM cortex intact	Left anterior basal ganglia (caudate nucleus, putamen, internal capsule), CC
342	Male	33	Traffic accident: severe blunt TBI	Bilateral frontal contusion: frontal pole and anterior FM cortex; focus on left lateral frontal pole (gyrus rectus, medial and anterior orbital gyrus bilaterally, and right lateral and posterior orbital gyrus)	Bilateral anterior temporal contusion
467	Female	40	AcoA aneurysm (ruptured): perioperative and postoperative (vasospastic) lesions	Left lateral frontal and lateral orbitofrontal (left, anterior, lateral, and posterior orbital gyrus, posterior part of medial orbital gyrus), left subcallosal FM cortex, right FM cortex, and medial orbitofrontal (right gyrus rectus and medial orbital gyrus)	Bilateral septal region, CC
589	Male	42	Fall: severe open TBI	Bilateral orbitofrontal and basal anterior FM cortex (left anterior gyrus rectus, medial and anterior orbital gyrus, right gyrus rectus, and medial orbital gyrus)	Traumatic hemorrhages left caudate nucleus and left minor forceps, left lateral precentral region, CC
FM group					
150	Male	28	Traffic accident: severe blunt TBI	Bilateral frontopolar and anterior orbitofrontal, bilateral anterior FM cortex (gyrus rectus, medial orbital, and anterior orbital gyrus bilaterally lesioned)	Minor contusion right inferior frontal and anterior temporal, traumatic microbleed left lower midbrain and left posterior thalamus
188	Male	38	Severe open TBI caused by a hit with a heavy object.	Bilateral frontopolar, right orbitofrontal (anterior parts of gyrus rectus and medial orbital gyrus bilaterally)	Minor right temporopolar lesion; initially, subarachnoid and peridural hemorrhage posterior fossa and left occipital convexity
203	Female	50	Olfactory meningeoma with large perifocal edema	Bilateral medial orbitofrontal and anterior FM cortex, medial frontal pole (anterior parts of gyrus rectus, and medial orbital gyrus bilaterally lesioned)	None
291	Male	39	Traffic accident: severe blunt TBI	Contusion of the left lateral frontal and frontopolar region, bilateral medial orbitofrontal (left anterior gyrus rectus, anterior medial orbital gyrus lesioned; left anterior, lateral, and posterior orbital gyri; right anterior gyrus rectus and anterior medial orbital gyrus)	Diffuse axonal injury; anterior and lateral temporal contusions

Downloaded from http://direct.mit.edu/jocn/article-pdf/8/4/363/1962329/jocn.1996.8.4.363.pdf by guest on 18 May 2021

Table 1. (*continued*)

Patient	*Sex*	*Age (Years)*	*Etiology*	*Lesion Sites*	*Accessory Lesions*
300	Male	39	Traffic accident: severe blunt TBI (1980)	Bilateral frontal and orbitofrontal contusions; frontal pole and anterior fm cortex bilaterally (gyrus rectus, medial and lateral orbital gyri bilaterally lesioned)	Left inferior frontal gyrus
480	Male	36	Traffic accident: severe blunt TBI	Bilateral orbitofrontal contusions (gyrus rectus, anterior parts of medial orbital gyrus lesioned)	Traumatic microbleeds fronto-lateral white matter and anterior insula bilaterally and splenium of CC, bilateral anterior temporal contusions, minor right fronto-lateral lesion (inferior frontal gyrus)
520	Male	47	Fall: blunt TBI	Bilateral frontal hemorrhagic contusions, medial and lateral orbitofrontal lesion bilaterally, left basal anterior FM cortex and right basal FM cortex and both frontal poles lesioned	Minor right anterior temporal contusion

AcoA = arteria communicans anterior; CC = corpus callosum; TBI = traumatic brain injury.

age of lesions in the lateral group was higher than in the medial group and vice versa. This demarcation can be described by a line running approximately parallel to the limb of the forceps minor from the anterior horn of the ventricle to the fronto-lateral convexity. The activation focus obtained for stimulus-driven dimension changes in non-brain-damaged participants was in the area that was dominantly affected by lesions in the LFP group. In contrast, the activation focus observed with top-down-controlled dimension changes was within the area dominantly affected by lesions in the FM group. Lesions in the right anterior prefrontal cortex were dominantly observed in the FM group. This, however, was because of our selection criterion: We selected only left hemispheric lesions in the lateral group, in keeping with our left LFP activation in normal participants.

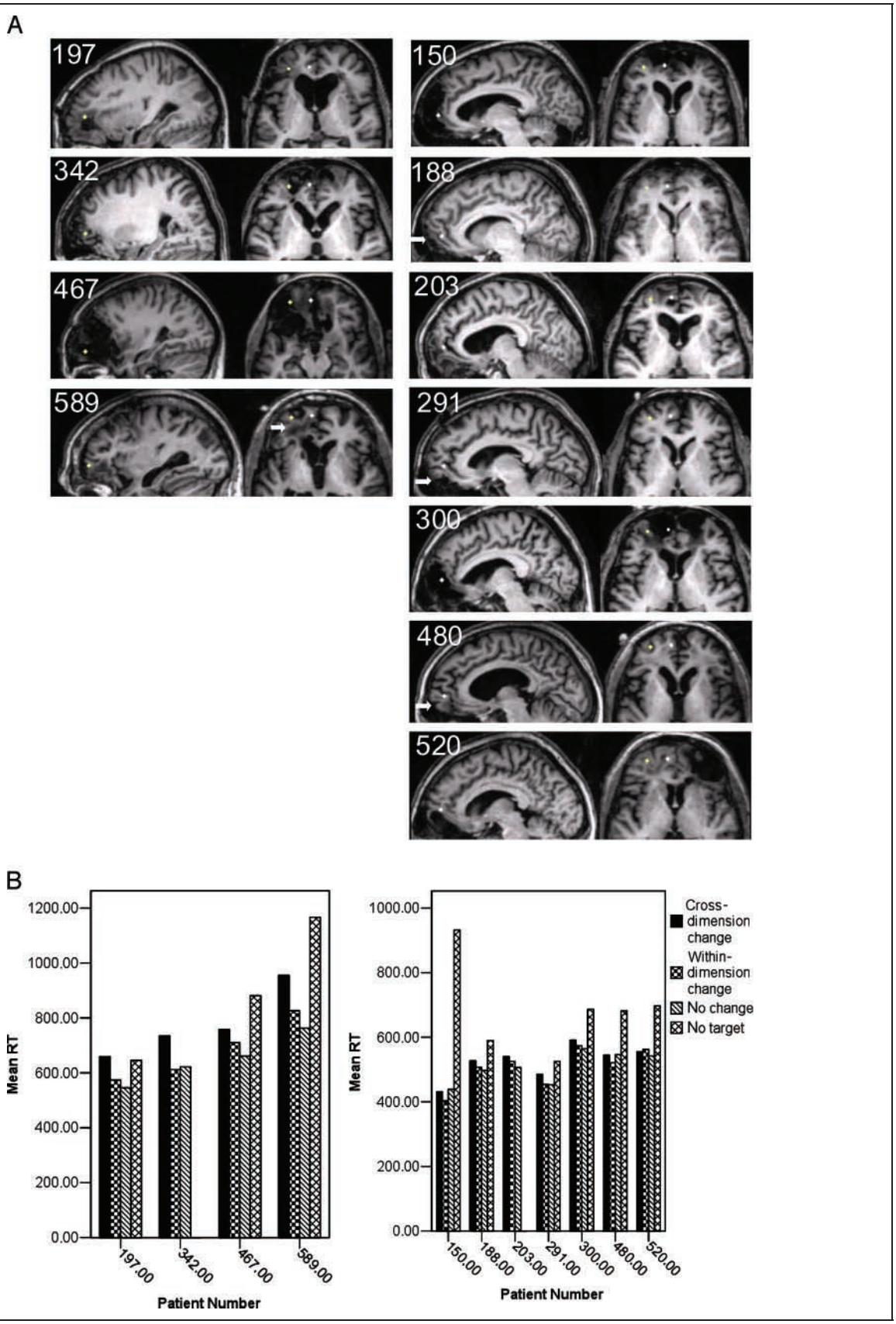
Stimuli and Procedure

Displays contained 5 × 5, 6 × 6, or 7 × 7 items. The latter displays extended 14° × 14° of visual angle. Displays consisted of green vertical bars, each sized 0.2° × 0.8°. In 50% of the trials, one of the green bars was replaced by a target. There were four different targets, two, red or blue vertical bars, defined by their color, and the other two, green bars tilted 45° to the left or the right, defined by their orientation. Targets and distractors of same luminance (4.3 cd/m^2) were presented on a black background (0.5 cd/m^2). Targets were presented equiprobably at all locations within the display matrix, with the exception of the outer borders. The experiment was run in a dimly lit room. Participants viewed the displays at a distance of 100 cm.

Displays were presented for maximally 5 sec or until a response was given. Participants responded with a forced-choice key press to target presence (right index finger) or target absence (left index finger). After an intertrial interval of 1500 msec, the next display was presented. Blocks of 48 trials were separated by breaks, the duration of which could be chosen by the participant (minimum 5 sec). The experiment consisted of 13 blocks. The first, practice, block of 24 trials contained all possible target types and display sizes. The data of this block were discarded. The remaining 12 blocks consisted of 6 cross-dimension search blocks with a total of 528 trials, which contained both color- and orientation-

Figure 1. Individual patient data. (A) Individual lesion location relative to the dimension change-related activation foci (indicated by white dots) in the left LFP and left FM cortex observed in participants without brain lesions in Experiment 2 of Weidner et al. (2002). The left column shows the patients with lateral anterior prefrontal lesions; the right column, the patients with FM lesions. Left hemisphere is on the left. (B) Individual mean response times for cross-dimensional change trials, within-dimensional feature-change trials, trials without change, and target-absent trials. Because of a technical problem, the target-absent RTs for two patients (203 and 342) were lost.

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/462/1962329/jocn.2007.19.3.462.pdf by guest on 18 May 2021



Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/365/1962239/jocn.2007.19.3.365.pdf by guest on 18 May 2021

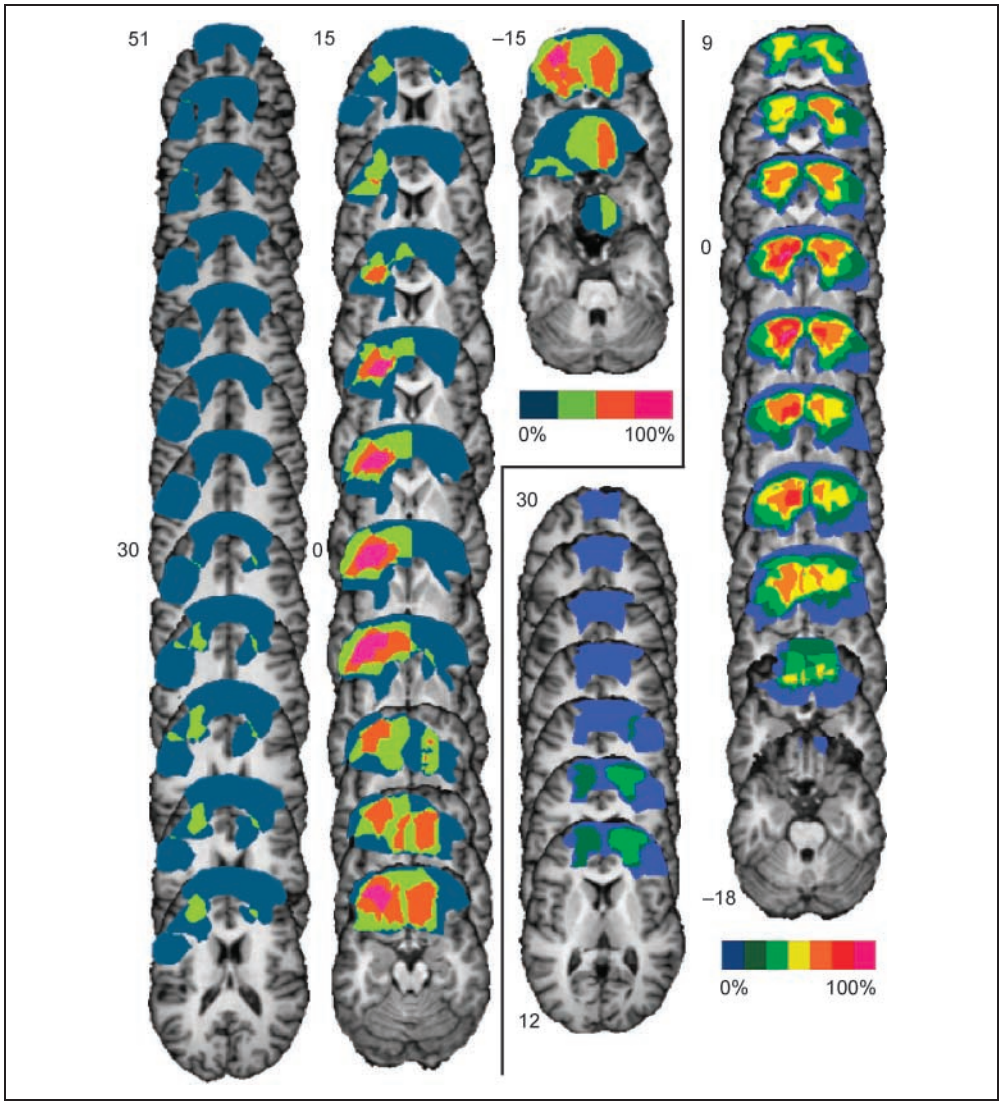


Figure 2. Lesion density maps of the lateral (left) and medial (right) anterior prefrontal patient groups. For each voxel, the percentage of patients with a lesion in the respective group is indicated by a color scale. Left hemisphere is on the left. Numbers indicate z coordinate in Talairach and Tournoux's (1988) reference frame.

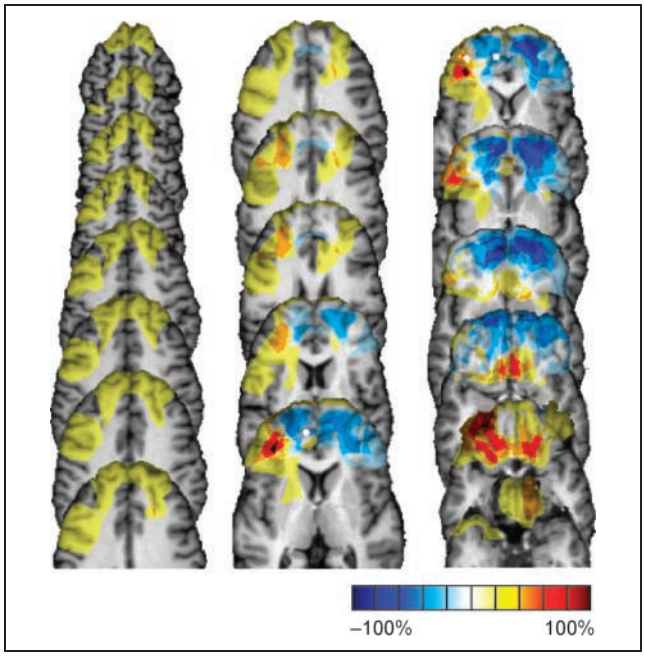


Figure 3. Lesion density maps of lateral versus medial anterior prefrontal lesions. Axial slices are shown in three columns, beginning on the top left with the most dorsal slice. For each voxel, the percentage of medial patients with a lesion was subtracted from the percentage of lateral patients with a lesion. The color scale shows 10 levels, and each bar represents 20% increments; thus, the darkest red represents areas that are lesioned in 100% of lateral and none of the medial patients. The middle white percentage bar designates regions where there was an identical percentage of lesions in both patient groups (0%). The dark blue regions are lesioned in 100% of medial and none of the lateral patients (−100%). The black dot in the upper right image represents the location of the frontopolar stimulus-driven dimension change-related activation maximum in a study with normal subjects (Weidner et al., 2002, Experiment 2). The white dot in the upper right and middle bottom images represents the FM top-down-controlled activation maximum in the same experiment. Left hemisphere is on the left.

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/365/1965375/jocn.2007.19.3.365.pdf by guest on 18 May 2021

defined targets. Of the remaining 6 within-dimension search blocks of 480 trials in total, 3 contained only color-defined targets and 3 only orientation-defined targets. Within blocks, the different trial types were presented in pseudorandomized order. The sequence of blocks was varied such that the same condition was not repeated in immediately successive blocks.

RESULTS

Behavioral Data

Based on our previous imaging studies, we expected increased stimulus-driven dimension change costs in patients with left LFP lesions, in contrast to patients with FM lesions. According to our hypothesis that the left LFP is specifically involved in visual dimension changes, we further expected that changes between target-defining features within a dimension would not lead to enhanced costs in the same patients. Accordingly, we carried out a repeated measures analysis of variance (ANOVA) on the change costs, with type of change (dimension vs. feature) as within-subjects factor and lesion location (LFP vs. FM) as between-subjects factor. Reaction times (RTs) were overall increased in the LFP patients (Figure 4A). Compared with the FM group, RTs in the no-change condition (hitherto referred to as baseline) was significantly increased [$t(9) = 3.46, p < .05$]. Therefore, in addition to the ANOVA on RT, we carried out an analogous ANOVA on percent RT change from baseline to remove confounding influences of overall RT performance. Both these ANOVAs yielded significant main effects for lesion location [RT: $F(1,9) = 22.32, p < .05$; percent change: $F(1,9) = 20.37, p < .05$] and change [RT: $F(1,9) = 57.41$, $p < .05$; percent change: $F(1,9) = 60.86, p < .05$] and a significant interaction [RT: $F(1,9) = 26.60, p < .05$; percent change: $F(1,9) = 21{,}68, p < .05$]. Figure 4B shows that patients with LFP lesions exhibited higher dimension change costs than patients with FM lesions. Both groups displayed higher dimension change costs than

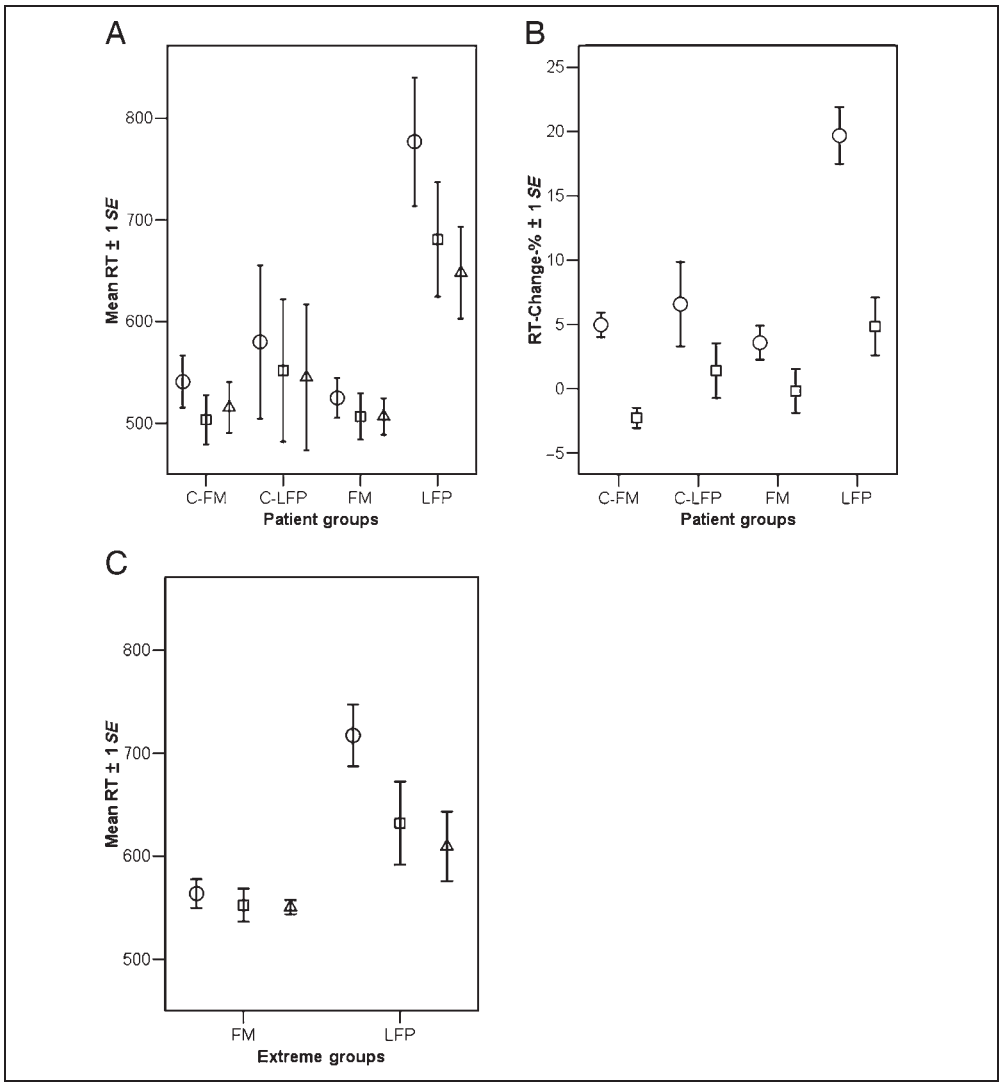


Figure 4. Group response times. (A) Mean response times in cross-dimension change trials (circle), within-dimension feature change trials (square), and no-change baseline (triangle) trials. (B) Mean cross-dimension change costs (circle) and within-dimension feature change costs (square) as percentage of the no-change baseline response time. (C) Same as (A), but for extreme groups with equal baseline response times (see text for details). C-LFP: control left frontopolar group; C-FM: control frontomedian group.

Downloaded from http://direct.mit.edu/jocn/article-pdf/14/3/363/1965375/089892902317361912.pdf by guest on 18 May 2021

feature change costs. The interaction reflected a differential increase in dimension change costs in LFP patients.

Conceivably, higher dimension change costs in LFP compared with FM patients may arise from decreased dimension change costs in the latter, rather than increased costs in the former, group. To rule out this possibility, we compared the search RTs of both patient groups with the RTs obtained for the matched non-brain-lesioned control groups. Compared with their normal controls, LFP patients displayed higher change costs overall and, specifically, increased dimension change costs (Figure 4B). ANOVAs with change type (dimension change vs. feature change) as within-subjects factor and group (LFP patients and controls) as between-subjects factor yielded significant main effects for group [RT: $F(1,6) = 7.70$, $p < .05$; percent change: $F(1,6) = 7.61$, $p < .05$] and change [RT: $F(1,6) = 24.83$, $p < .05$; percent change: $F(1, 6) = 27.9$, $p < .05$] and a significant interaction [RT, $F(1,6) = 7.32$, $p < .05$; percent change: $F(1,6) = 6,53$, $p < .05$].

In contrast, FM patients did not differ from their normal controls in overall change costs [RT, $F(1,12) = .08$, $p > .05$; percent change, $F(1,12) = .05$, $p > .05$]. Dimension changes led to higher costs than feature changes [RT: $F(1,12) = 59.46$, $p > .05$; percent change: $F(1,12) = 55,7$, $p < .05$], with dimension change costs being comparable in both groups (4% increase in patients, 5% in controls). Relative to feature change costs, dimension change costs were actually higher in the control group, resulting in a significant Change Type × Group interaction [RT: $F(1,12) = 6.97$, $p > .05$; percent change: $F(1,12) = 5,57$, $p < .05$].

Only a few errors were made in both the patient and the control groups. As Levene's test for equality of variances did not indicate any significant violations of this assumption, two-tailed t tests for equal variances were calculated. The two patient groups did not differ significantly in either percent total errors [LFP vs. FM: 2.1% vs. 1.4%; $t(9) = 0.71$, $p < .05$] or misses [LFP vs. FM: 2.5% vs. 2.3%; $t(9) = 0.08$, $p > .05$], but the LFP patients made more false alarms [LFP vs. FM: 1.6% vs. 0.4%; $t(9) = 2.27$, $p < .05$]. The LFP patients displayed a higher percentage of total errors compared with their control group [CLFP: 0.2%; $t(6) = 2.86$, $p < .05$], although neither the miss (CLFP: 0.2%) nor the false-alarm rate (CLFP: 0.3%) comparisons were significant [$t(6) = 1.43$, $p > .05$, and $t(6) = 2.00$, $p > .05$, respectively]. The FM patients did not differ from their control group in either total errors [CFM: 1.2%; $t(12) = 0.19$, $p > .05$], misses [CFM: 1.9%; $t(12) = 0.34$, $p > .05$], or false alarms [CFM: 0.6%; $t(12) = 0.51$, $p > .05$]. Finally, both control groups did not differ significantly in total errors [$t(9) = 1,82$, $p > .05$], misses [$t(9) = 1.40$, $p > .05$], or false alarms [$t(9) = 0.71$, $p > .05$].

The specific pattern of increased dimension change costs for LFP, compared with FM, patients—which was the same whether performance was analyzed in terms of RT or percent RT change—argues against causation by unspecific slowing of response times in the former group. However, to investigate this issue even further, we compared patients in both lesion groups with comparable baseline RTs: the three LFP patients with the shortest baseline RTs and the three FM patients with the highest baseline RTs. Baseline RTs were not significantly different between these groups [$t(4) = 1.71$, one-tailed $p > .05$). Nevertheless, the ANOVA on RTs with the factors group (LFP, FM) and change type (dimension, feature) yielded significant main effects for group [$F(1,4) = 22.01$, $p < .05$] and change type [$F(1,4) = 16.65$, $p < .05$] and, most importantly, a significant Group × Change Type interaction [$F(1,4) = 9.77$, $p < .05$], underlining the selectively increased RTs on cross-dimension change trials for LFP patients (Figure 4C; dimension change costs: LFP = 108 msec, FM = 13 msec; feature change costs: LFP = 22.61 msec, FM = 1.78 msec).

DISCUSSION

Based on previous fMRI experiments with non-brain-injured participants (Weidner et al., 2002; Pollmann et al., 2000), we hypothesized that the left LFP would be involved in shifts of attention between visual dimensions. Here, we tested this hypothesis by examining dimension change costs in a visual singleton feature search task in patients with frontopolar lesions. We found increased dimension change costs in patients with left LFP lesions, compared with patients with FM lesions as well as with non-brain-injured controls. This pattern converges with the dimension change-related LFP increase of the fMRI signal in non-brain-injured participants and supports our hypothesis that the left LFP is genuinely involved in stimulus-driven visual dimension weighting.

Most accounts of frontopolar function are based on tasks making complex cognitive demands. Accordingly, they postulate frontopolar contributions to high-level cognitive processing, such as ''cognitive branching,'' the combining of working memory retention with dual-task processing (Koechlin, Corrado, Pietrini, & Grafman, 2000; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999), the use of self-generated information (Christoff, Ream, Geddes, & Gabrieli, 2003), or the integration of multiple higher cognitive processes (see Ramnani & Owen, 2004, for a review). At first sight, all of these accounts fail to explain the finding of frontopolar dimension change-related activation in our singleton feature search paradigm, which is neither demanding on working memory (see Müller, Krummenacher, & Heller, 2004) nor on executive functions. However, there are parallels between these accounts and our paradigm. Dimension changes in singleton feature search require changes (although attentional shifts rather than task shifts) and an interaction of attention with memory

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/462/1962329/jocn.2007.19.3.462.pdf by guest on 18 May 2021

(episodic rather than working memory), as we will discuss subsequently.

Lateral Frontopolar Cortex and Change-related Behavior

We propose that the left LFP supports changes of attention when the need to shift attention is not explicitly indicated by specific stimulus attributes (e.g., an arrow pointing to the target location) or task instructions. We have demonstrated dimension change-related activation in the left LFP in singleton feature search (Weidner et al., 2002; Pollmann et al., 2000). The selective increase of dimension change costs in the LFP patients in the current study supports the notion that this structure facilitates the shift of attentional resources from the old to the new target-defining dimension.

However, the frontopolar cortex appears to support attention changes only under specific conditions. Anterior prefrontal cortex was not usually related to shifts of (visuospatial and featural) attention in previous imaging studies. One characteristic of cross-dimensional singleton search that sets it apart from most previous studies of attention shifts is that the target-defining dimension on a given trial is undetermined. In standard visual search, participants are instructed to search for a specific target (e.g., a red X). When a change occurs, participants are typically informed in advance. This is different in singleton search. Here, participants have to discern the presence of an odd-one-out stimulus, but they do not know exactly how the singleton will differ from the distractors. In particular, uncertainty about the dimension that will contain the unique target-defining feature gives rise to RT costs in detecting the singleton (see Found & Müller, 1996; Müller et al., 1995, 2004, who reasoned that singleton feature detection in cross-dimensional search requires at least implicit determination of the target-defining dimension). Moreover, adopting a singleton search mode, as compared with a set for a specific feature target, leaves observers open to distracting effects of salient stimuli in task-irrelevant dimensions (Bacon & Egeth, 1994). It may be that the left frontopolar cortex contributes to this openness for salient stimuli in currently noncritical dimensions, which have been ''irrelevant'' (i.e., distractors) in the past, but may become ''relevant'' (i.e., targets) in the future. This might explain why change-related frontopolar activation is observed in singleton search, but not in search for predetermined targets (e.g., a green × among various kinds of distractors).

Anterior prefrontal activation has been observed in other change paradigms that share a component of ambiguity, for example, the target-defining dimensions in the Wisconsin Card Sorting Test (Nagahama et al., 2001; Rogers, Andrews, Grasby, Brooks, & Robbins, 2000; Grant & Berg, 1948), or ambiguous word primes in cued recall (Henson, Shallice, Josephs, & Dolan, 2002). In a review of the literature, Burgess, Simons, Dumontheil, and Gilbert (2005) conclude that rostral prefrontal lesions ''disproportionately impair performance in 'ill-structured' situations,. . .where the optimal way of behaving is not precisely signalled by the situation'' (p. 209). Taken together, this evidence may suggest that anterior prefrontal cortex is involved in the active search for relevant information within a predetermined space of potential options.

Lateral Frontopolar Cortex and Episodic Memory

Detection of task-relevant changes (e.g., a change in the target-defining dimension) requires the comparison of stimulus attributes (such as the color and movement direction of the singleton) between the current and the previous trial. The frontopolar cortex is reliably activated during this kind of episodic memory retrieval (Christoff & Gabrieli, 2000; Rugg & Wilding, 2000). Furthermore, activation strength in the frontopolar cortex correlates with the amount of proactive interference (Henson et al., 2002), which may also indicate that the frontopolar cortex is involved in change detection. A comparison between previous and current stimulus characteristics may be especially important in tasks that permit automatic processing to maintain the ability to respond optimally to changes in the environment. Such a comparison depends on what has been termed *source memory*, that is, memory under what circumstances a particular item was encoded. Recently, the left frontopolar cortex, although more lateral and inferior than the activations found in our studies, was reported to support source memory selectively (Dobbins, Foley, Schacter, & Wagner, 2002). More posterior left inferior frontal areas, by contrast, showed activations related to both source and item memory.

Left LFP activation was also observed in tasks requiring the recollection of contextual information, specifically, the task in which a particular item was previously encountered. In contrast, no frontopolar activation was found for the recollection of the list membership of repeated items, underlining the specificity of the frontopolar involvement in the recollection of task-related details (Simons, Owen, Fletcher, & Burgess, 2005). These findings fit well with the concept of task-related change detection in the left LFP, which, in turn, leads to a shift of attentional resources to adapt to a change in task demands. Our data fit into this framework if task-related information is not narrowly seen as related to switching operations between tasks, but also to attentional weight shifts within the same task, in our case, singleton feature search.

To conclude, we observed a specific increase in dimension change costs in a visual singleton feature search task in patients with left lateral anterior prefrontal lesions, compared both with patients with anterior FM lesions and controls without brain lesions. This finding

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/2/369/1962329/jocn.2007.19.2.369.pdf by guest on 18 May 2021

agrees with dimension change-related activation in previous event-related fMRI studies with normal subjects and supports our proposal that the left LFP is involved in the change of attention from the old to the new target-defining dimension in singleton feature search. The specific role of this brain area in attention changes may be episodic change detection, which enables the organism to reallocate attentional resources according to changing task demands. This specific hypothesis, however, needs to be investigated in further research.

Reprint requests should be sent to Stefan Pollmann, Institut für Psychologie II, Otto-von-Guericke-Universität, Postfach 4120, D-39016 Magdeburg, Germany, or via e-mail: stefan.pollmann@nat.uni-magdeburg.de.

Note

1. This study is restricted to the investigation of singleton feature search. We found that singleton conjunction search is too demanding to be carried out in patients.

REFERENCES

Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics, 55,* 485–496.

Beauchamp, M. S., Cox, R. W., & DeYoe, E. A. (1997). Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *Journal of Neurophysiology, 78,* 516–520.

Büchel, C., Josephs, O., Rees, G., Turner, R., Frith, C. D., & Friston, K. J. (1998). The functional anatomy of attention to motion. *Brain, 121,* 1281–1294.

Burgess, P. W., Simons, J. S., Dumontheil, I., & Gilbert, S. J. (2005). The gateway hypothesis of rostral prefrontal cortex (area 10) function. In J. Duncan, L. Phillips, & P. McLeod (Eds.), *Measuring the mind: Speed, control, and age* (pp. 217–248). Oxford: Oxford University Press.

Christoff, K., & Gabrieli, J. D. E. (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology, 28,* 168–186.

Christoff, K., Ream, J. M., Geddes, L. P., & Gabrieli, J. D. (2003). Evaluating self-generated information: Anterior prefrontal contributions to human cognition. *Behavioral Neuroscience, 117,* 1161–1168.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21,* 761–773.

Culham, J. C., Brandt, S. A., Cavanagh, P., Kanwisher, N. G., Dale, A. M., & Tootell, R. B. H. (1998). Cortical activation produced by attentive tracking of moving targets. *Journal of Neurophysiology, 80,* 2657–2670.

Dobbins, I. G., Foley, H., Schacter, D. L., & Wagner, A. D. (2002). Executive control during episodic retrieval: Multiple prefrontal processes subserve source memory. *Neuron, 35,* 989–996.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96,* 433–458.

Found, A., & Müller, H. J. (1996). Searching for unknown feature targets on more than one dimension: Investigating a ''dimension-weighting'' account. *Perception & Psychophysics, 58,* 88–101.

Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S., Kim, Y. H., Meyer, J. R., et al. (1999). A large-scale distributed network for covert spatial attention: Further anatomical delineation based on stringent behavioural and cognitive controls. *Brain, 122,* 1093–1106.

Grant, D. A., & Berg, E. A. (1948). A behavioural analysis of degree of reinforcement and ease of shifting to new responses in a Weigl-type card sorting problem. *Journal of Experimental Psychology, 38,* 404–411.

Henson, R. N. A., Shallice, T., Josephs, O., & Dolan, R. J. (2002). Functional magnetic resonance imaging of proactive interference during spoken cued recall. *Neuroimage, 17,* 543–558.

Koechlin, E., Basso, G., Pietrini, P., Panzer, S., & Grafman, J. (1999). The role of the anterior prefrontal cortex in human cognition. *Nature, 399,* 148–151.

Koechlin, E., Corrado, G., Pietrini, P., & Grafman, J. (2000). Dissociating the role of the medial and lateral anterior prefrontal cortex in human planning. *Proceedings of the National Academy of Sciences, U.S.A., 97,* 7651–7656.

Lepsien, J., & Pollmann, S. (2002). Covert reorienting and inhibition of return: An event-related fMRI study. *Journal of Cognitive Neuroscience, 14,* 127–144.

Liu, T., Slotnick, S. D., Serences, J. T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex, 13,* 1334–1343.

Luks, T. L., & Simpson, G. V. (2004). Preparatory deployment of attention to motion activates higher-order motion-processing brain regions. *Neuroimage, 22,* 1515–1522.

Müller, H. J., Heller, D., & Ziegler, J. (1995). Visual search for singleton feature targets within and across feature dimensions. *Perception & Psychophysics, 57,* 1–17.

Müller, H. J., Krummenacher, J., & Heller, D. (2004). Dimension-specific inter-trial facilitation in visual search for pop-out targets: Evidence for a top-down modulable visual short-term memory effect. *Visual Cognition, 11,* 577–602.

Nagahama, Y., Tomohisa, O., Katsumi, Y., Hayashi, T., Yamauchi, H., Oyanagi, C., et al. (2001). Dissociable mechanisms of attentional control within the human prefrontal cortex. *Cerebral Cortex, 11,* 85–92.

Pollmann, S. (2001). Switching between dimensions, locations, and responses: The role of the left frontopolar cortex. *Neuroimage, 14,* S118–S124.

Pollmann, S. (2004). Anterior prefrontal cortex contributions to attention control. *Experimental Psychology, 51,* 270–278.

Pollmann, S., & Morrillo, M. (2003). Left and right occipital cortices differ in their response to spatial cueing. *Neuroimage, 18,* 273–283.

Pollmann, S., Weidner, R., Müller, H. J., & von Cramon, D. Y. (2000). A fronto-posterior network involved in visual dimension changes. *Journal of Cognitive Neuroscience, 12,* 480–494.

Pollmann, S., Weidner, R., Müller, H. J., & von Cramon, D. Y. (2006). Neural correlates of visual dimension weighting. *Visual Cognition, 14,* 877–897.

Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience, 5,* 184–194.

Rogers, R. D., Andrews, T. C., Grasby, P. M., Brooks, D. J., & Robbins, T. W. (2000). Contrasting cortical and subcortical activations produced by attentional-set shifting and reversal learning in humans. *Journal of Cognitive Neuroscience, 12,* 142–162.

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/365/1965375/jocn.2007.19.3.365.pdf by guest on 18 May 2021

Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Sciences, 4,* 108–115.
Simons, J. S., Gilbert, S. J., Owen, A. M., Fletcher, P. C., & Burgess, P. W. (2005). Distinct roles for lateral and medial anterior prefrontal cortex in contextual recollection. *Journal of Neurophysiology, 94,* 813–820.
Talairach, P., & Tournoux, J. (1988). *A stereotactic coplanar atlas of the human brain.* Stuttgart: Thieme.
Vandenberghe, R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2001). Functional specificity of superior parietal mediation of spatial shifting. *Neuroimage, 14,* 661–673.
Weidner, R., Pollmann, S., Müller, H. J., & von Cramon, D. Y. (2002). Top–down controlled visual dimension weighting: An event-related fMRI study. *Cerebral Cortex, 12,* 318–328.
Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., et al. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience, 5,* 995–1002.

Downloaded from http://direct.mit.edu/jocn/article-pdf/19/3/365/1962329/jocn.2007.19.3.365.pdf by guest on 18 May 2021