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Neural Correlates of Visual Dimension Weighting

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Abstract

In a series of functional magnetic resonance experiments, we have investigated the neural basis of attentional dimension weighting in cross-dimensional singleton search. Previous studies led to the characterization of a fronto-posterior network of brain areas, which in part overlaps with the fronto-parietal network supporting overt and covert attention shifts, but also involves anterior prefrontal components, which are likely to be involved in the detection of change and the initiation and control of attention shifts. While this frontoposterior network is characterized by transient dimension change-related activation, we present new evidence that the effect of attentional weighting of a target-defining dimension is a modulation of the visual input areas processing the attended dimension.

Introduction

In visual search for salient singleton-feature items, search costs are observed when the feature by which the target differs from the nontarget objects on a given trial is defined in a different visual dimension to that on the preceding trial (e.g., a colour-defined target following a motion-defined target; Found and Müller, 1996). In contrast, no such change costs are observed when the target is defined by a different feature within the same dimension (e.g., a red target following a blue target). To explain this pattern of results, Müller, Heller and Ziegler (1995) proposed a 'dimension-weighting' account, according to which there is a limit to the total amount of attention, or attentional weight (cf. Duncan & Humphreys, 1989), available to be allocated to objects' dimensions. Potential target-defining dimensions (i.e., dimensions in which the target might differ from the nontarget objects) are assigned weight in accordance with their variability across trials. Target detection is facilitated when attentional weight is allocated to the target-defining dimension to amplify the target's saliency signal generated within this dimension (cf. Cave & Wolfe, 1990; Wolfe, 1994). In the case of salient targets defined by a deviant single feature (as described above), the allocation of attention weight to the target-defining dimension is largely stimulus-driven. Dimension changes incur a cost because they involve a shift of attention weight from the old to the new dimension. A more detailed account of the behavioural research on visual dimension weighting is presented by Müller and Krummenacher (this volume).

Functional imaging of visual dimension weighting. In a series of event-related functional magnetic resonance imaging (fMRI) studies, we have investigated the neural basis of attentional changes between visual dimensions (Pollmann, Weidner, Müller & von Cramon, 2000; Weidner, Pollmann, Müller & von Cramon, 2002; Pollmann, Weidner, Müller & von Cramon, 2004). In this paper, we review the central findings from these studies and present new data on the attentional modulation of dimension-specific visual input areas during visual singleton-feature search across target-defining dimensions. Figure 1 gives an overview of the dimension change-related activation patterns.

Fronto-posterior network activated during dimension changes. In our first fMRI study on visual dimension weighting, we investigated the network of brain areas involved in visual dimension changes (Pollmann et al., 2000). Participants performed visual singleton-feature searches while lying in the magnetic resonance tomograph. One goal of this study was to measure phasic activation increases related to changes in the target-defining dimension from the previous to the current trial. Such phasic dimension change-related increases in the blood-oxygenation-level-dependent (BOLD) response were observed in a number of brain areas across the cerebral cortex. This network consisted of many areas that have consistently been reported to be involved in visual search or shifts of visual attention, including visual areas of the occipital lobe in fusiform gyrus, lateral occipital gyri and cuneus; precuneus, superior parietal lobule and supramarginal gyrus in the parietal lobe; and middle temporal gyrus and posterior superior temporal sulcus in the temporal lobe. One major component of the frontoparietal network, the frontal eye fields, though displaying activity in comparison of search trials versus fixation, has consistently failed to show dimension change-related activation in our studies. This may indicate that FEF supports visuo-spatial, rather than dimensional, attention changes. In addition, we found change-related activation in left frontopolar cortex and, less pronounced, in pregenual

frontomedian cortex at the rostral border of anterior cingulate cortex.

These data indicated that a large part of the network that supports visual search and covert as well as overt visual attention shifts (e.g., Corbetta, Akbudak, Conturo, Snyder, Ollinger, Drury, Lineweber, Petersen, Raichle, van Essen & Shulman, 1998; Donner, Kettermann, Diesch, Ostendorf, Villringer & Brandt, 2002; Gitelman, Nobre, Parrish, LaBar, Kim, Meyer & Mesulam, 1999; Kastner, Pinsk, De Weerd, Desimone & Ungerleider, 1999; Nobre, Sebestyen, Gitelman, Mesulam, Frackowiak & Frith, 1997; Müller et al. 2003; Pollmann & von Cramon, 2000) was phasically involved in visual dimension changes. In addition, anterior prefrontal areas, which were not typically found to be involved in visual attention shifts, were also involved in visual dimension changes (see Pollmann, 2001, and Pollmann, 2004, for a detailed discussion of the contribution of anterior prefrontal cortex to visual dimension weighting). The finding that a large-scale network, particularly including prefrontal cortex, which is ususally related to executive functions, was activated by visual dimension changes was non-trivial, as the task to be performed was efficient, 'pop-out', search of singleton-feature targets. However, the increased neural change-related activity indirectly measured by the change-related BOLD-signal increases paralleled the increased search reaction times (RTs) manifest when the target-defining dimension changed (rather than remaining the same) from the previous to the current trial.

These dimension change costs occurred despite the fact that the target-defining dimension was irrelevant for the response, which was simply to elicit a speeded target-present versus target-absent reaction regardless of the target-defining dimension. Furthermore, the costs occurred despite the targets being highly salient, so that attentional weighting of the targetdefining dimension may not have been strictly necessary for detection (though weighting did make search more efficient when the target dimension remained the same across successive trials). In this situation, changes in the attentional weight setting are likely to be driven externally by changes in

the target-defining dimension, rather than internally by intention. In two further experiments, we examined a task that involved endogenously controlled changes in dimensional weighting, and compared the neural networks supporting endogenously and exogenously driven changes (Weidner et al., 2002).

Endogenously controlled visual dimension weighting. Endogenously controlled dimension weighting was investigated in a singleton conjunction search task that followed the same logic as the singleton feature search used by Pollmann et al. (2000). The target was defined by the conjunction of a feature in a constant, primary dimension (always size) and a feature in a variable, secondary dimension (colour or motion). In contrast to singleton feature search, singleton conjunction search was inefficient, indicated by slow search RTs. Singleton conjunction search led, again in contrast to singleton feature search, to increased activation along the superior frontal sulcus, dominantly in the right hemisphere. The major difference in the change-related activation elicited by both experiments was a double dissociation between a change-related increase of frontopolar activation in singleton feature, but not singleton conjunction search, and the reverse, a selective dimension change-related activation in singleton conjunction, but not singleton feature search, in pregenual frontomedian cortex (Weidner et al., 2002; indicated by the red spots in Figure 1). In more posterior brain areas, dimension change-related activation was elicited mostly within the same anatomical structures in both types of task. Posterior parietal activation, however, reflected more general (rather than specifically dimension) change-related processes, evidenced by comparable activations related to dimension changes and intra-dimensional feature changes (Weidner et al. 2002).

We hypothesised that the prefrontal areas activated following dimension changes, the left frontopolar cortex and the pregenual frontomedian cortex, were involved in the control of attentional weight shifting between visual dimensions and that high-level ‘visual’ areas in parietal

and temporal cortices mediate these attention shifts via feedback to dimensionspecific visual input areas.

Modulation of dimension-specific visual input areas. The dimension-weighting account postulates that a change in the target-defining dimension initiates a shift in the allocation of attention from the old to the new dimension (Found & Müller, 1996). Accordingly, we expected to see a modulation of the activation in visual input modules for the target-defining dimensions colour and motion. In our first experiment, we observed such an attentional modulation in that the activation increased in bilateral fusiform foci when the participants attended to colour as the target-defining dimension (Pollmann et al., 2000). The location of the activation focus was concordant with previous reports of area V4, which is involved in colour processing (e.g., McKeefry & Zeki, 1997; for a review, see Bartels & Zeki, 2000). When targets were instead defined by motion direction, an increase in activation was observed in lateral occipital cortex (dominantly on the right) at locations in the vicinity of the human MT+ complex (hMT+[1]), which responds to moving stimuli (e.g., Beauchamp, Cox & DeYoe 1997). Thus, attending to colour or motion led to increased activation in brain areas that are involved in processing the respective target-defining visual dimension.

These attentional modulations of V4 and hMT+ activity were obtained in a comparison of experimental blocks in which the targets were constantly defined within a given visual dimension: colour in one block, motion in the other (see also Corbetta, Miezin, Dobmeier, Shulman & Petersen, 1991). The dimension-weighting account, however, assumes a shift of attentional weight from the old to the new dimension, which starts with a change in the target-defining dimension (e.g., from colour to motion) and then persists across trials until the next dimension change (from motion to colour). To investigate attentional dimension weighting in

[1] The term hMT+ indicates that the human activation data may represent area MT or other motion processing

areas, such as MST, hence MT+. 7

crossdimensional search, the data of a new fMRI experiment were analysed for evidence of attentional modulation in dimension-specific visual input modules. Unlike the previous studies, the present experiment used a 'compound' search task in which participants had to detect the presence of a singleton colour or, respectively, motion target in the display, but give a two-alternative forced-choice response based on a form feature of the target (i.e., the information required for the response was independent of that required for detecting the target). Krummenacher, Müller and Heller (2002) had shown that the typical dimension change effects (cf. Found & Müller, 1996) are also obtained in compound tasks, although they are reduced relative to simple detection tasks. The advantage of using a compound task for the purposes of the present experiment was that no target-absent trials were required. This permitted not only an event-related analysis of target dimension change versus no-change trials, but also an analysis of trial 'epochs' (uninterrupted by target-absent events) with colour targets versus 'epochs' with motion targets.

Methods

Participants. Twenty-one observers (9 female) took part in a single fMRI experimental session. They ranged between 21 and 37 years in age, with a mean age of 26.4 years. All observers were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The fMRI-procedures were approved by the University of Leipzig ethics committee. All observers gave prior written informed consent according to the guidelines of the Max Planck Institute.

Stimuli, Task, Design and Procedure. Stimuli were displayed by an LCD projector on a back-projection screen mounted in the bore of the magnet behind the participant's head. Participants viewed the screen wearing mirror glasses, which were equipped with corrective

lenses if necessary.

The fMRI session began with the presentation of a 30-s fixation period, followed by the presentation of 624 experimental trials, and ending with a 30-s fixation period. Trial 8 duration was 1.5 s. Each trial began with the presentation of a search display. The display was terminated by the participant's response or after a maximum duration of 1.5 s. A white fixation cross was displayed during the inter-trial interval, which was, variably, 0, 500 or 1000 ms in duration. The experiment used a 2 x 2 factorial design, with the factors dimension change (yes/no) and response change (yes/no). Trials from each of the four cells of the design matrix were presented with a probability of .2, the remaining trials were null events, that is, fixation periods of the same length as the experimental trials. The order of events, including null events, was determined using maximum-length shift register sequences (m-sequences; for a detailed description, see Buracas & Boynton, 2002), which counterbalance sub-sequences of a given length in order to ensure that trials from each condition were preceded equally often by trials from each of the other conditions.

The visual search displays consisted of 25 triangles on a black background. The stimuli were arranged in a grid-like pattern, covering an area of 13° x 13° of visual angle. Each triangle pointed randomly in one of two directions, equally often to the left and the right (Figure 2). All stimuli moved sinusoidally along the horizontal axis (maximum amplitude = 0.2°, speed = 1.2°/s). Each search display contained a singleton pop-out target, which was equally likely to be defined by a unique colour relative to the nontargets (a red horizontally moving triangle among green horizontally moving triangles) or by a unique motion direction (a green triangle moving along an oblique axis tilted oriented +45° from the horizontal among horizontally moving green triangles).

Participants were asked to give a speeded forced-choice response, indicating the

pointing direction of the target triangle, using their right-hand index (left button) or middle finger (right button).

fMRI Measurement. Functional images were collected at 3T by a Bruker 30/100 Medspec system (Bruker Medizintechnik, Ettlingen, Germany), using a gradient echo EPI sequence (TR = 2000 ms, TE = 30 ms, flip angle = 90°). Twenty axial slices were acquired parallel to the AC-PC plane, allowing for whole brain coverage. Slice thickness was 4 mm and interslice distance 1 mm, with a 19.2-cm FOV and a 64 x 64 image matrix. Data were analysed using the LIPSIA software package (Lohmann et al., 2001). Slice acquisition time differences were corrected by sinc interpolation. Movement artefacts were corrected using a matching metric based on linear correlation. Baseline drifts were corrected by high-pass filtering, implemented using a discrete Fourier transform with an individually tailored cut-off period of five times the mean temporal distance between trials of the same experimental condition. In the spatial domain, the data were filtered using a Gaussian filter with FWHM = 7 mm. Following this preprocessing, the functional data sets were co-registered with the individual participants' high-resolution anatomical data sets and normalized by linear scaling. Data were analyzed using the general linear model (Friston, Holmes, Worsley, Poline, Frith & Frackowiak, 1995). Epoch-based analyses were performed using a half-sine fixed response model. The begin of colour epochs was defined by a change from motion to colour as the target-defining dimension (i.e., the onset of a search display containing a colour-defined target when the previous trial contained a motion-defined target). Colour epochs ended at the next change from colour to motion (i.e., the onset of a display with a motion-defined target following a display with a colour-defined target). Motion epochs were defined accordingly. Group activation was calculated using a random-effects model (Holmes & Friston, 1998). We

tested for increased activation during epochs in which colour was the target-defining dimension in the posterior fusiform gyrus and increased activation during epochs in which motion was the target-defining dimension in the lateral occipital gyrus. The significance criterion for these region-of-interest (ROI) analyses was α=0.01.

Results

Behavioural data. Reaction times (RTs) and error rates have been evaluated separately for colour- and motion-target trials. RTs for the colour trials were significantly faster (700 ms) compared to the motion condition (722 ms; paired t-test: $t(2) = 4.0831$, $p < 0.001$). Error rates were low overall and did not differ between conditions (colour=3.5%; motion=3.1%; paired ttest: $t(20) = -0.4295$, n.s.).

A repeated-measures ANOVA of the RT data, with the factors dimension change (change, no change) and response change (change, no change), only revealed the interaction to be significant ($F(1,20)=7.6$, $MS_e=2366$, $p<0.05$). Collapsed across response change conditions, there was no significant RT increase for trials on which the target dimension changed (relative to the preceding trial) compared to no-change trials, 713 versus 709 ms (non-significant main effect of dimension change, $F(1,20)=2.8$, $MS_e=278.55$, $p>0.05$). Likewise, RTs, collapsed across dimension change conditions, were not significantly increased for response change compared to no-change trials, 714 ms versus 708 ms (nonsignificant main effect of response change, $F(1,20)=3.3$, $MS_e=722.3$, $p>0.05$).

In the absence of a response change, changes in the target dimension significantly slowed RTs (715 and 701 ms for dimension change and no-change trials, respectively; $t(20) =2.8$, $p<0.05$); in contrast, when there was a response change, RTs tended to be faster when the target dimension changed, too (710 and 717 ms, respectively; $t(20)= 1.97$, $p= 0.06$). In the absence of a dimension change, changes in the response significantly slowed RTs (717 and 701 ms for

response change and no-change trials, respectively; $t(20)= 3.3$, $p<0.01$); however, when there was a dimension change, RTs were somewhat, though not significantly faster when the response changed as well (710 and 715 ms for response change and no-change trials, respectively; $t(19)= 0.93$, $p>0.05$). This interactive pattern of dimension change and response change effects is robust: the same pattern was observed in a reanalysis of the compound-task RT data of Krummenacher, Müller and Heller (2002; see Müller & Krummenacher, 2005 [this volume]).

Error rates were low overall (3.2%). In order to rule out that the RT-effects were due to speed-accuracy trade-offs, the error data were examined by an analogous, dimension change (change, no change) x response change (change, no change), ANOVA. This ANOVA revealed only the interaction to be significant (dimension change: $F(1,20)=0.63$, $MS_e=0.01$, n.s; response change: $F(1,20)=0.031$, $MS_e=0.004$, n.s.; dimension change x response change: $F(1,20)=7.46$, $MS_e=0.21$, $p<0.05$). In the absence of a response change, there was a trend towards higher error rates on dimension change compared to no-change trials (3.5% versus 2.8 %, $t(20)= 1.78$, $p=0.9$), while in the presence of response change, there were significantly lower error rates on dimension change trials (2.7% vs. 3.9%, $t(20)=2.51$, $p<0.05$). This pattern of error effects reinforces the RT effects.

Functional-imaging data. In order to investigate the attentional modulation in extrastriate visual areas processing colour and motion, we compared the activation in epochs with colour as the target-defining dimension to the activation in epochs with motion as the target dimension. To increase the power of the comparisons, we focused on two regions of interest (ROIs) that we had previously observed to exhibit attentional modulation in singleton feature search (Pollmann et al., 2000). One of these areas was the posterior fusiform gyrus, which contains the human area V4 (our previous activations for sustained attention at x=-23, y=-64, z=-7 and x=22, y=-76, z=-16, corresponding to the location of posterior V4, according to Bartels &

Zeki, 2000); the other one was an area in lateral occipital cortex, around the bifurcation of the inferior temporal sulcus in its ascending and posterior descending limbs, which contains the hMT+ complex (Dumoulin, Bittar, Kabani, Baker, Le Goualher, Bruce Pike & Evans, 2000). Previously, we found activations for sustained attention to motion somewhat more anteriorly at x=41, y=-52, z=-2 (Pollmann et al., 2000). Note, though, that Beauchamp et al. (1997), reviewing fMRI studies of motion processing, reported a more posterior average location of hMT+ at x=+/-42, y=-70, z=-3.

We expected increased activation during colour epochs in posterior fusiform gyrus and increased activation during motion epochs in lateral occipital cortex. In line with our expectations, we found a significantly increased activation during colour epochs compared to motion epochs in the right posterior fusiform gyrus bordering the collateral sulcus (x=13, y=-89, z=-3; Z_{max}=2.58; Figure 3). Motion epochs exhibited increased activation compared to colour epochs in lateral occipital cortex at x=37, y=–78, z=-8 (Z_{max}=2.41).

The analyses of dimension-change versus response-change-related imaging data are presented in a separate paper (Pollmann, Weidner, Müller & von Cramon, 2004).

Discussion

The interaction of anterior prefrontal cortices and visual posterior areas, presumably mediated by fronto-parietal and fronto-temporal back projections, is of great interest for understanding the neural basis of visual attention. In previous studies, we described a fronto-posterior network of brain areas that was phasically active during changes of the targetdefining dimension in visual singleton search. In the following sections, we will discuss the evidence revealed in the present study on visual dimension weighting in occipital areas for colour and motion processing, and go on to consider the fronto-posterior network involved in visual

dimension weighting and possible contributions of its component structures. A schematic representation of this network is given in Figure 4, and Table 1 provides a summary of our imaging data on visual dimension weighting.

One central finding of our previous studies was that, in addition to the fronto-parietal network supporting visual search and covert visual attention shifts, frontopolar areas exhibited dimension change-related activation. Specifically, in singleton feature search, dimension changes were associated with increased left lateral frontopolar activation in the vicinity of the intermediate frontal/frontomarginal sulcus; by contrast, in singleton conjunction search, dimension changes were associated with pregenually located frontomedian activation. In both types of search task, dimension changes resulted in RT costs, which, on the dimensionweighting account, reflect the reallocation of attentional weight from the old to the new targetdefining dimension. However, these weight shifts are induced in different ways in the two tasks. In singleton feature search, the change in the target-defining dimension is triggered by the salient target itself. By contrast, in singleton conjunction search, the dimension change proceeds under top-down control, when the search process fails to discern the presence of a target in the previously weighted (secondary) dimension.

The present study. The present results provide further evidence for the dimension-weighting account. Both electrophysiological work in the monkey and human imaging studies have shown that attending to a location, stimulus feature or object may lead to a modulation of activity in visual cortex (for a recent review, see Treue, 2003). In our previous experiments, we have observed a signal increase in the fusiform gyri at the location of human posterior V4 when colour was the target-defining dimension throughout a block of trials, and in lateral occipital gyrus, somewhat anterior to the human MT+ complex, when motion was the targetdefining dimension (Pollmann et al., 2000).

These modulations of activation, however, may have been due to sustained attention over whole blocks of trials, rather than shifts of attention from the old to the new targetdefining dimension in cross-dimensional search, as postulated by the dimension weighting account. Therefore, in the present experiment, we compared the activation obtained during epochs in cross-dimensional search in which successive targets were defined in the colour versus the motion dimension. We observed increased activation in right posterior fusiform gyrus when colour, rather than motion, was the target-defining dimension. The reverse pattern, increased activation during motion epochs compared to colour epochs, was observed in right lateral occipital gyrus. The fusiform signal increase during colour epochs was located slightly posterior to the location of posterior V4 according to a review of colour processing studies (Bartels & Zeki, 2000). The signal increase during motion-defined epochs agreed well with previous reports of the location of hMT+. However, both colour and motion-related activations were located more posteriorly than the activations we previously observed for sustained attention to colour and motion. It is not clear whether this merely reflects anatomical variability or differences in the experimental design between studies, or whether sustained attention and attentional dimension shifts in cross-dimensional search activate neighbouring, but distinct neuronal ensembles. In any case, our data show that activation in dimensionspecific input modules of extrastriate cortex is systematically modulated depending on the target-defining dimension in cross-dimensional singleton feature search. The modulations were dimension-specific and did not reflect general influences of processing time. Although responses were overall faster to colour than to motion targets, the signal increases for colour targets in the fusiform and for motion targets in the lateral occipital gyri were symmetric. This pattern of modulations is may be taken to support the dimension-weighting account, according to which a change in the target-defining dimension entails a shift of attention from the old to the new target-defining dimension.

One possible objection is that, in principle, the activation differences between colour and motion epochs may reflect bottom-up effects resulting from the presence of colour and, respectively, motion singletons in the two types of epoch. This is unlikely, however, because the search displays used in the present experiment provided strong inputs into both colour and motion processing areas: participants were exposed to the onset of 25 coloured triangles (all green, except for one possible red singleton) that were all moving sinusoidally (all oscillating along the horizontal axis, except for one possible diagonally moving singleton). Given the massive color and motion signals produced by the 25 display elements, it is unlikely that the presence of a colour or motion singleton exerted a major impact on the bottom-up activation of V4 or hMT+. This reasoning is supported by the fact that we failed to observe any changerelated activation differences when we investigated different singleton targets within the same dimension, although the target colour or motion changed (red and blue targets in the presence of green distractors and left and right diagonally moving targets in the presence of horizontally moving distractors; Pollmann et al., 2000) which might have led to stimulus-induced activation changes in V4 or hMT+.

Each trial contained a target, either defined by a singleton color or motion. This means that, according to the dimension weighting account, attention was constantly allocated either to the colour or motion dimension. This means that we cannot distinguish whether increased activation in V4 and hMT+ was due to signal increase when attention was allocated to the preferred dimension, signal decreases when attention was directed at the alternative dimension, or a mixture of both. Future experiments may clarify this issue by introducing a third condition, e.g. orientation-defined targets, in which attention is withdrawn from both colour and motion.

Anatomical connectivity and recurrent processing. Neuroanatomical connectivity studies have revealed long connections from the prefrontal cortex to reach the posterior parietal cortex,

the temporal lobe (superior, inferior temporal regions, and the superior temporal sulcus) and the paralimbic areas (Pandya , Dye & Butters, 1971). In monkeys, ventral BA10 (which includes the site of frontopolar dimension change-related activation in our studies with humans) is connected with visual association area VA2 (Pandya & Yeterian, 1985). Since the human homologue of VA2 is not known, one can only speculate that the posterior fusiform and lateral occipital gyri are part of it and target sites of back projections from the frontopolar region. It is, at least, plausible that back projections from frontopolar regions are targeted to second- and third-order, rather than first-order, visual association cortices.

It is well established that long association connections from frontal and parietal cortices to extrastriate visual areas are involved in visual attention (Felleman & van Essen, 1991; Lewis & van Essen, 2000). Electrophysiological and human imaging studies have shown these reciprocal connections to be used for both bottom-up and top-down processing within the context of selective attention (Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000; Noesselt, Hillyard, Woldorff, Schoenfeld, Hagner, Jäncke, Tempelmann, Hinrichs & Heinze, 2002). The rapid interplay between bottom-up and top-down processes is difficult to analyze non-invasively in the human brain, because of temporal limitations with fMRI and uncertainties with localizing the sources of electrical and magnetic encephalographic signals.

Dimension change processes and dimension-specific processing. However, in our fMRI studies of visual dimension weighting, we found two temporally distinct response patterns. A large fronto-posterior network, extending from frontopolar cortex via higher-order visual association cortices to extrastriate visual cortex, was phasically activated following visual dimension changes. This dimension change-related activation pattern (which is accompanied by an increase in search RTs) indicates a transient increase in neural activity that, according to the dimension-weighting account, reflects a process of reallocating attention from the old to the new

dimension. The second activation pattern, revealed in the present study, varies on a slower timescale, in that activation increased when colour became the target-defining dimension and remained at an increased level until the next motion-defined target was presented. This activation was observed in posterior fusiform and lateral occipital gyri and is likely to reflect the outcome of the dimension-weighting process: increased activation in a colour-sensitive visual area for the duration of the period in which colour was the target-defining, attended dimension and increased activation in a motion-sensitive area when motion was the target-defining dimension.

It is more difficult to distinguish the contributions of the component areas within the dimension change-related network. However, among the areas with a change-related signal increase, one can distinguish between those areas that belong to the well-described frontoparietal network subserving shifts of visual attention and visual search (Corbetta et al. 1998; Donner et al., 2002; Gitelman et al., 1999; Müller et al., 2003; Nobre et al., 1997; Pollmann et al., 2000; Pollmann & von Cramon, 2000; Weidner et al., 2002) and those that do not belong to this network. It is likely that the former areas, in particular, those along the intraparietal sulcus and in the superior parietal lobule, are involved in executing shifts of attention between visual dimensions (Corbetta & Shulman, 2002; Yantis, Schwarzbach, Serences, Carlson, Steinmetz, Pekar & Courtney, 2002), which give rise to increased activation in visual input areas that analyse the attended dimension.

Role of anterior prefrontal cortex in dimension weighting. One question remains: What is the functional significance of the dimension change-related activation in those areas that do not belong to the traditional fronto-parietal network subserving visual attention, specifically: the left frontopolar cortex in the case of stimulus-triggered dimension changes and pregenual frontomedian cortex in the case of top-down controlled changes?

A potential contribution of frontopolar cortex to visual dimension weighting may be the

detection of task-relevant changes under conditions of stimulus ambiguity. Anterior prefrontal activation has also been observed in other paradigms that involve a component of uncertainty, for example, with ambiguous target-defining dimensions in the Wisconsin Card Sorting Test (WCST; Grant & Berg, 1948; Rogers et al., 2000; see also Nagahama et al., 2001, who differentiated changes related to the stimulus dimension, which involved anterior prefrontal cortex, from switches of stimulus-response associations, which activated posterior prefrontal cortex) and ambiguous word primes in cued recall (Henson, Shallice, Josephs & Dolan., 2002). Taken together, this evidence suggests that anterior prefrontal cortex is involved in the search for relevant information under conditions of uncertainty. Selection of relevant information under uncertainty may also be a contributing factor to the real world problems in planning and execution of multiple task sequences (Burgess, Veitch, de Lacy Costello & Shallice, 2000; Goel et al., 1997) and prospective memory (Burgess, Quayle & Frith, 2001) in patients with anterior prefrontal lesions.

Note that our participants were not explicitly instructed to switch attention or respond in any specific way to visual dimension changes. Rather, dimension weighting seems to take place implicitly when the target-defining dimension changes (see also Müller, Krummenacher & Heller, 2004). Shifting attentional weight from the old to the new target-defining dimension may not be strictly necessary, given the 'pop-out' character of the targets. But such weight shifts can be advantageous, expediting detection RTs on dimension repetition, relative to dimension change, trials. However, in order to initiate an attention shift, the task-relevant change in the display, in our case: in the target-defining dimension, must be registered first, and this requires the (episodic) comparison of stimulus attributes, in our case: the color and movement direction of the singleton, between the current trial and the previous trial. There is evidence that frontopolar cortex plays a role in this process.

Frontopolar cortex is reliably activated during retrieval from long-term memory (Christoff & Gabrieli, 2000; Rugg & Wilding, 2000), which is an important prerequisite for an episodic comparison of present and past trials. A comparison between previous and current stimulus attributes may be especially important in tasks that permit (semi-)automatic processing, in order to maintain the flexibility to respond adequately to changes in the environment. Such a comparison depends on what has been termed 'source memory': the memory under what circumstances a particular item was encoded. Recently, Dobbins, Foley, Schacter and Wagner (2002) reported left frontopolar cortex (though more lateral and inferior than the activations reviewed above) to support source memory selectively, whereas more posterior left inferior frontal areas exhibited activations related to both source and item memory. However, the task of Dobbins et al. required explicit recollection of the circumstances of encoding, in contrast to present visual singleton search task, which may be a reason for the differential locations of activation in frontopolar cortex between the two tasks. Nevertheless, the distinction between anterior inferior frontal activation (extending into frontopolar cortex) associated with source memory, and more posterior inferior frontal activation associated with both source and item memory is potentially important. It suggests that left anterior prefrontal cortex may have a specific role in episodic memory, which may be utilized for the control of attention whenever the task requires search for an ambiguously defined target, involving shifts of attention between visual dimensions.

Conclusion

Changes in the target-defining dimension in visual singleton search lead to a transient activation in an extensive fronto-posterior network of brain areas. This network consists of areas in parietal and temporal cortex, that are known to support shifts of attention, and of anterior prefrontal areas, particularly the lateral frontopolar cortex ant the pregenual frontomedian cortex,

that may be involved in the detection of change and the initiation and control of attention shifts. These attention shifts express themselves in terms of modulations in dimension-specific visual input areas, which take the form of an elevated activation that is maintained over trials as long as the target-defining dimension remains constant.

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Figures

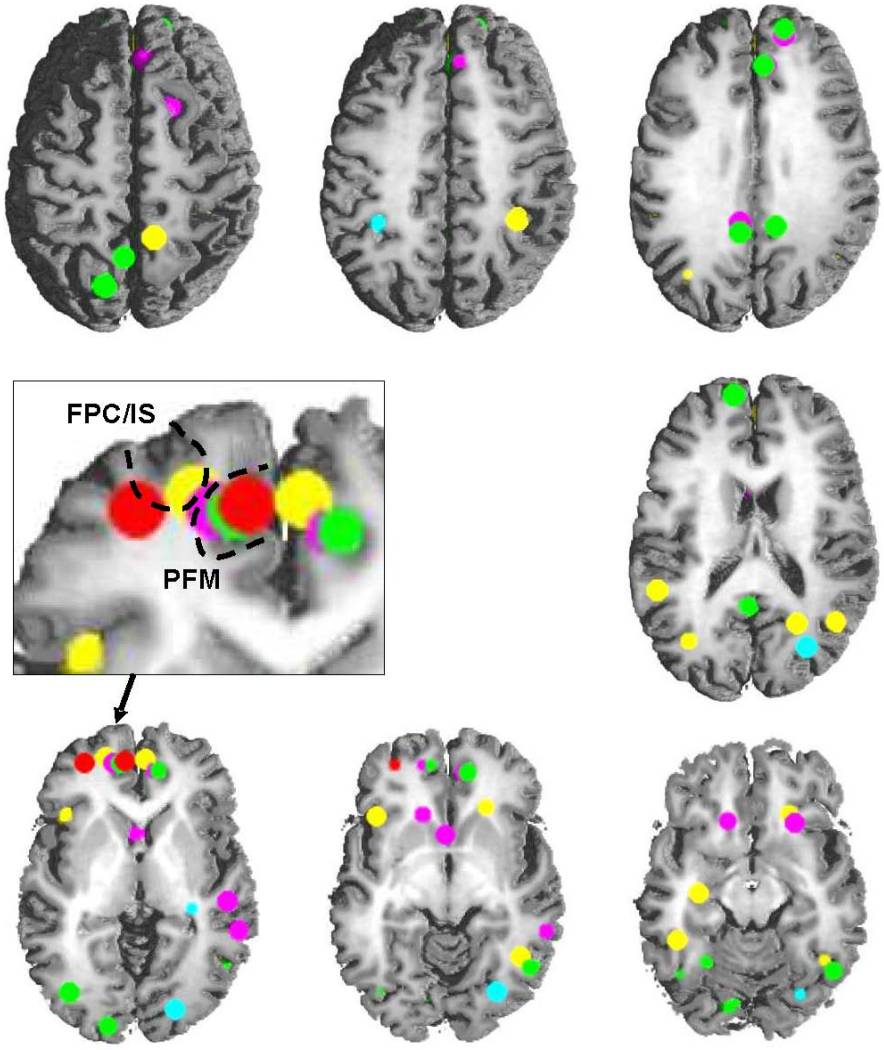
Figure 1: Overview of activation patterns obtained in our series of event-related fMRI experiments on visual dimension weighting. For singleton feature searches, the main effect of dimension change is represented by yellow (Pollmann et al., 2000) and, respectively, blue spots (Pollmann et al., submitted). For singleton conjunction search, the main effect of dimension change is represented by green spots and the interaction dimension change (present, absent) x search type (cross-dimension, within-dimension) by purple spots (Weidner et al., 2002, Experiment 1). The interaction search task (singleton feature, singleton conjunction) x dimension change (present, absent) is represented by red spots (Weidner et al., Experiment 2). The spots are centred on the points of maximum activation. The maximum is set to a standard value for all loci, rather than representing the actual activation strengths. Inserted is an enlarged view of left

anterior prefrontal cortex (FPC/IS: frontopolar cortex/intermediate sulcus; PFM: pregenual frontomedian cortex).

Figure 2: Search displays. Search displays consisted of a matrix of (5 x 5 =) 25 triangles that pointed randomly to the left or right. In each display, one triangle, the target, differed from the others, the distractors: either by its colour (red, indicated by black in the figure, as compared to green, indicated by grey) or its direction (axis) of sinusoidal motion (45° oblique as compared to horizontal).Participants had to detect the odd-one-out target triangle and make a button press response indicating the target's pointing direction (left or right).

Figure 3: a) Increased activation for epochs with colour as the target-defining dimension compared to motion as the target-defining dimension in right fusiform gyrus (x=13, y=-89, z=-3; coordinates of Talairach & Tournoux, 1998). b) Increased activation for epochs with motion as the target-defining dimension compared to colour as the target-defining dimension in right lateral occipital gyrus (x=37, y=–78, z=-8). The colour scale of the activation overlays represents z-values. Left hemisphere is on the left.

Figure 4: Schematic illustration of the dimension-weighting network. Core anatomical structures activated during visual dimension changes are shown on the left, putative associated functions on the right. The arrows between boxes indicate potential bottom-up and recurrent connections between areas. Due to the complexity of the network, the indicated connectivity is unlikely to be complete. STS: superior temporal sulcus; MTG: middle temporal gyrus; IPS: intraparietal sulcus; SPL: superior parietal lobule; hMT+: human MT+ complex.



Dimension change in singleton feature search (main effect)
Dimension change in singleton feature search (main effect)
Dimension change in singleton conjunction search (main effect)
Interaction of search (cross/within dimension) x change in singleton conjunction search
Interaction of search type (conjunction, feature) x change

Fig. 1

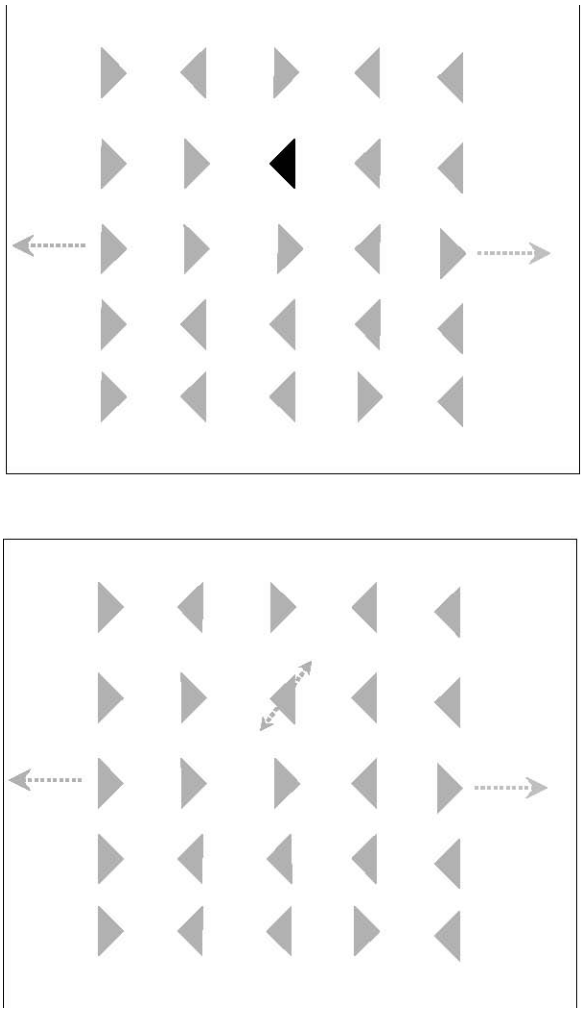
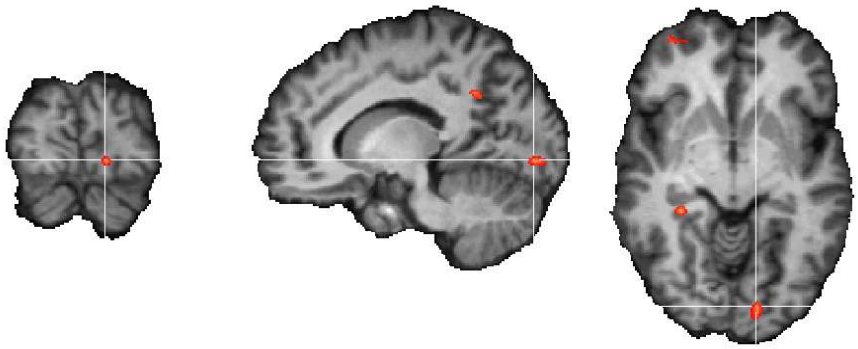


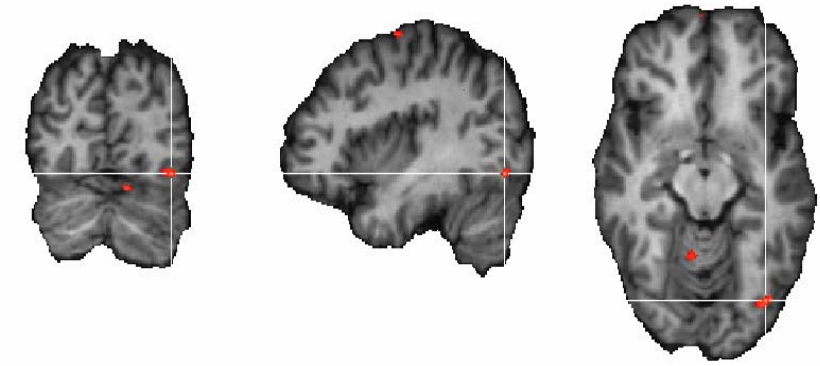
Fig. 2

Fig. 3

a) Colour - Motion



b) Motion - Colour



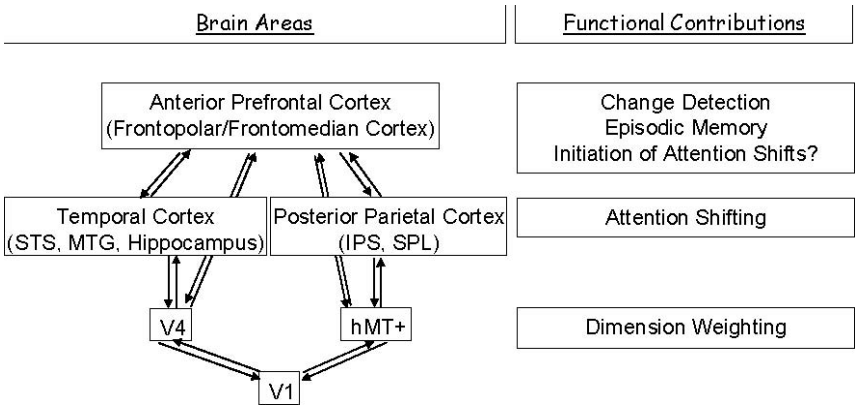

Brain Areas
Functional Contributions
Anterior Prefrontal Cortex
(Frontopolar/Frontomedian Cortex)
Change Detection
Episodic Memory
Initiation of Attention Shifts?
Temporal Cortex
(STS, MTG, Hippocampus)
Posterior Parietal Cortex
(IPS, SPL)
Attention Shifting
V4
hMT+
Dimension Weighting
V1

Fig. 4