Top-down Controlled Visual Dimension Weighting: An Event-related fMRI Study

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Target detection in visual singleton feature search is slowed when consecutive targets are defined in different visual dimensions. Behavioral data provide evidence that attentional weight needs to be shifted between dimension-specific processing modules. We found similar dimension-specific change effects in a conjunction search task, in which observers searched for an odd-one-out target defined by a unique combination of size and color or, respectively, size and motion direction. Changes of the secondary target dimension (color or motion) across trials, but not target feature changes within a dimension, increased the time required to detect the target. Dimensional change costs were greatly increased for singleton conjunction search compared to singleton feature search. This suggests involvement of top-down control processes in dimensional change in conjunction search, in contrast to stimulus-driven dimensional change in singleton feature search. The functional anatomical correlates of top-down controlled visual dimension changes were investigated in two event-related functional magnetic resonance imaging (fMRI) experiments. In Experiment 1, dimensional change in singleton conjunction search was accompanied by transient activations in a fronto-posterior network of brain areas that was largely non-overlapping with the general network activated during visual search. Experiment 2, which contrasted singleton feature and conjunction search within the same session, revealed a double dissociation in anterior prefrontal cortex: left frontopolar cortex was selectively involved in stimulus-driven dimension changes but not in top-down controlled dimension changes, whereas the reverse was observed in frontomedian cortex.

Introduction

Visual processing in the human brain is massively parallel, generating a detailed representation of our surroundings, including information about the shape, color, size, distance (depth), relative position and motion of surfaces, and objects within the scene (Marr, 1982). When there are multiple objects in the scene, a problem arises: that of selecting those entities for limited-capacity visual processing and the control of visually guided action that are relevant to the current goals of the organism. The mechanisms by which visual selection is accomplished have been referred to by the summary term 'visual attention'. Over several decades of visual attention research, three main types of visual attention theory have developed: space-based, object-based and dimension-based. Space-based theories propose that attention is directed to spatial regions or locations of the visual field (Posner, 1980). Object-based theories assume that selection operates on perceptually delineated and integrated object representations (Duncan, 1984). Dimension-based theories propose that selection is limited by the nature of the required discriminations between different stimulus attributes, more precisely, between categories or dimensions of attributes (Allport, 1971).

A novel account of dimension-based visual attention has recently been proposed (Müller, *et al*., 1995; Found and Müller,

1996), based on visual search experiments in which observers had to detect the presence of a singleton (odd-one-out) feature target in a display, under conditions in which the target-defining dimension varied randomly across trials (cross-dimension search). Under conditions of dimensional uncertainty, in which the target-defining dimension was variable, target detection was slowed compared to conditions in which the target-defining dimension was fixed; in contrast, uncertainty about the target-defining feature within a given dimension did not produce any reaction time (RT) costs. Furthermore, dimension-specific inter-trial effects were observed; that is, detection of a target on a given trial was slowed when the target-defining dimension changed from the preceding to the current trial, but not when the target feature changed with the dimension remaining constant.

Müller and his colleagues took the cross-dimension search cost and dimension-specific inter-trial effects to argue for a dimension-weighting account of visual search for singleton feature targets. According to this account, detection of a feature target requires that attentional weight is allocated to the corresponding dimension-specific input module, to amplify its saliency signal on an integrating master map of activations, on which detection responses are based (Cave and Wolfe, 1990; Wolfe, 1994). The dimensional weight-pattern established in this process persists into the next trial, producing a dimension-specific RT advantage for a target defined within the same dimension as the preceding target.

There is behavioral evidence that, in simple singleton feature search tasks of the type described above ('pop-out' tasks), the target-defining dimension is determined and weighted relatively automatically, without involving deliberate (top-down) control operations (H.J. Müller *et al*., submitted for publication). While little top-down control may be required in singleton feature search, top-down control processes may have to come into play in more complex tasks in which singleton targets are defined by a unique combination of features in multiple dimensions (singleton conjunction search task).

The aims of the present study were twofold: (i) to examine behaviorally whether dimension weighting extends to cross-dimensional singleton conjunction search and (ii) to investigate the functional neuroanatomy underlying dimension-weighting processes in such complex search tasks and contrast it with that revealed in singleton feature search (Pollmann *et al*., 2000).

The new search task in the present study required observers to detect a target defined by a conjunction of size and either color or motion. Displays contained items, filled-in squares, that were either large or small in size, red versus blue or green in color, and sinusoidally oscillating diagonally (lower right–upper left versus lower left–upper right) or horizontally in motion direction. In this way, cross-dimension and within-dimension conditions could be realized analogously to the simple singleton

feature search tasks mentioned above (Müller *et al.*, 1995; Pollmann *et al.*, 2000).

If the dimension-weighting processes that were revealed in simple singleton feature search tasks (Müller *et al.*, 1995; Found and Müller, 1996; Pollmann *et al.*, 2000) extend to these more complex singleton conjunction search tasks, essentially the same pattern of effects with regard to the secondary target-defining dimension was expected, in particular: (i) an RT cost for cross-dimension search relative to within-dimension search and (ii) an RT cost for dimension change (relative to no-change) trials, but not for feature change (relative to no-change) trials. Furthermore, if dimension-weighting processes require a greater degree of deliberate, top-down control in singleton conjunction search compared to singleton feature search, the cross-dimension search costs and inter-trial effects would be expected to be increased in magnitude (despite overall slower detection RTs).

A recent study of the functional neuroanatomy of singleton feature search (Pollmann *et al.*, 2000) found dimension changes across trials (as compared to no-change trials) in cross-dimension search to activate a brain network consisting of left frontopolar cortex and inferior frontal gyri, which may be involved in the control of attentional weight shifting, as well as high-level visual processing areas in parietal and temporal cortex, probably mediating attentional allocation to extrastriate visual areas processing the target dimension. The latter hypothesis was supported by the finding that visual areas involved in the processing of color and movement, respectively, were activated when observers searched within the respective dimension.

Concerning singleton conjunction search across dimensions, similar structures were expected to be activated, although more strongly (Pollmann and von Cramon, 2000), to those activated in singleton feature search. The main issue of interest, however, concerned whether and to what extent, the network of brain areas supporting top-down controlled dimension weighting in singleton conjunction search would differ from that involved in stimulus-driven weighting in singleton feature (pop-out) search (Pollmann *et al.*, 2000).

There are grounds to expect major changes in the activation of frontal cortex structures involved in the control of visual dimension weighting, reflecting functional differences between stimulus-driven and top-down controlled attentional weighting processes. Superior frontal lesions have been found to impair the endogenous allocation of visuo-spatial attention (Koski *et al.*, 1998), and superior frontal gyrus has recently been reported to be massively involved in the top-down control of spatial attention (Hopfinger *et al.*, 2000). Superior frontal gyrus (BA9) activation was also manifest in our study of dimension weighting in singleton feature (pop-out) search (Pollmann *et al.*, 2000), which may indicate that superior frontal cortex is not exclusively involved in the control of visuo-spatial attention. However, our activation was related to cross-dimensional target variability as such (i.e. a divided-attention set) and not directly to dimensional change. Nevertheless, superior frontal cortex may be revealed to be involved in dimensional change in the current task, which is likely to require top-down control of attention weight shifts from the old to the new dimension.

Another area that may be shown to play a role in the top-down control of visual dimension weighting is the frontomedian wall. Recently, a distinction was proposed between the lateral and medial parts of anterior prefrontal cortex (Koechlin *et al.*, 2000), according to which stimulus-driven task control involves the lateral part of frontopolar cortex, whereas top-down control involves the frontomedian wall, including the medial surface of the superior frontal gyrus (F1) (Duvernoy, 1999) and the

pregenual portion of the anterior cingulate gyrus (ACC). In fact, our previous study, in which dimension change was triggered by singleton feature (pop-out) stimuli, revealed significant change-related left frontopolar activation, whereas activation around the pregenual portion of the cingulate sulcus (BA 32/24) appeared primarily related to cross-dimensional variability as such. However, weak dimensional change-related signal increases were also evident in the frontomedian wall.

The present study consisted of two functional magnetic resonance imaging (fMRI) experiments. Experiment 1 was designed to establish the network involved in top-down controlled dimension changes. If the distinction between stimulus-driven control processes in lateral and top-down control processes in medial anterior prefrontal cortex is correct, one would expect lateral frontopolar cortex to play a minor role in Experiment 1, whereas the frontomedian wall should display significant involvement in top-down controlled dimension change. The follow-on Experiment 2 was designed to contrast cross-dimensional singleton feature (pop-out) search with conjunction search, to permit a direct comparison between stimulus-driven and top-down controlled dimension changes.

Materials and Methods

Participants
Ten observers (five male, five female) aged between 21 and 31 years (mean age 23.7 years) took part in fMRI Experiment 1. Eight new observers (four female, four male) aged between 22 and 29 years (mean age 25.5 years) took part in Experiment 2. All observers were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The experiments were approved by the University of Leipzig ethics committee. All observers gave prior informed consent according to the guidelines of the Max Planck Institute.

Stimulus Presentation
Stimuli were displayed by an LCD projector on a back-projection screen mounted in the bore of the magnet behind the participants' heads. Observers viewed the screen wearing mirror glasses, which were equipped with corrective lenses if necessary.

In Experiment 1, fMRI sessions consisted of six scans. Each scan began with the presentation of a 30 s fixation period, followed by four stimulus- blocks. Blocks were separated by a 12 s fixation period. Each scan ended with a 30 s fixation period. A block lasted 90 s and included 30 trials of 3 s duration. A trial began with stimulus presentation. The stimulus display was terminated by the observer's response or after a maximum duration of 2.5 s. A white fixation cross was displayed from the termination of the display until the beginning of the next trial.

In Experiment 2, fMRI sessions consisted of one scan, starting with a 30 s fixation period, followed by ten stimulus blocks, and ending with a 30 s fixation period. A block lasted 180 s and consisted of 60 trials of 3 s duration each. The stimulus display was presented for 2.5 s, independently of the observer's response.

Stimuli, Task, Design and Procedure
In Experiment 1, stimuli consisted of 25 colored, large and small squares on a black background. Large and small squares subtended 0.6 × 0.6° and 0.4 × 0.4° of visual angle, respectively. The square color was variable and could be red, blue, or green. The elements were arranged in a grid-like pattern, covering an area of 13 × 13°, with some spatial jittering to prevent collinear groups forming in the display (Fig. 1). All stimuli moved sinusoidally in one of three possible directions (maximum amplitude = 0.2°, speed = 1.2°/s): along the horizontal axis or one of the diagonal axes (oriented ±45° relative to the horizontal axis). To avoid perceptual grouping of items moving in the same direction, a random phase shift was added to the sinusoidal movement.

A target was defined by a unique combination of its size (first dimension) and a second dimension, which could be either color or motion direction. Observers performed under three different conditions. In two within-dimension conditions, the second target-defining dimension was

constant (either color or motion). In a cross-dimension condition, the second target-defining dimension varied randomly across trials. In one within-dimension condition, observers had to search for a large square which could be colored either red or blue (within color). In the other within-dimension condition, they had to search for a large square moving in a direction oriented +45° or –45° relative to the horizontal (within

Figure 1. Illustration of a display containing a color-target (top). Target stimuli in the three experimental conditions (bottom). The first target-defining dimension was constant for all experimental blocks, i.e. targets were always large. In the within-color condition, targets differed from the large distractors in the color-dimension, i.e. they were either red or blue (bottom left); in the within-motion condition, targets differed from the large distractors in their (oscillating) motion direction, either +45° or –45° (bottom middle). In the cross-dimension condition, targets were either red or oscillating in –45° direction (bottom right).

motion). In the cross-dimension condition, observers had to search for a large square which either moved in a motion direction +45° from horizontal or was red (Fig. 2).

Target items were present on 60% of the trials. The two alternative targets within a block were presented equally frequently. Observers were asked to give a speeded forced-choice response, indicating the presence or absence of a target stimulus using their right-hand index or middle finger, respectively. A target-present response was to be made whatever the definition of the target within a block.

The session was subdivided into two halves, each presenting blocks of all three conditions in randomized order. Thus, two scans of functional data were acquired for each condition.

In Experiment 2, trial blocks were divided into two halves. In one half, stimuli were identical to the cross-dimensional conjunction search condition of Experiment 1. In the other half, distractor items were homogeneous in order to produce target pop-out (cross-dimensional feature search condition). All distractor squares were large and green and moved sinusoidally along their horizontal axis. As in the cross-condition, observers had to search for a large target that was either red or moved in a direction of motion +45° from horizontal.

Half of the observers started with the singleton feature search condition and half with the conjunction condition. In both conditions, blocks also included 20% null-event trials on which no search display was presented (and no response was to be made).

fMRI Measurement

Functional images were collected at 3 T by a Bruker 30/100 Medspec system (Bruker Medizintechnik, Ettlingen, Germany), using a gradient echo EPI sequence (T_R = 2000 ms, T_E = 30 ms, flip angle = 90°). In Experiment 1, 16 axial slices were acquired parallel to the AC–PC plane, allowing for whole brain coverage. Slice thickness was 5 mm, interslice distance 2 mm, with a 19.2 cm FOV and a 64 × 64 image matrix. In Experiment 2, 28 slices were acquired parallel to the AC–PC plane. Slice thickness was 4 mm, interslice distance was 1 mm, with a 19.2 cm FOV and a 64 × 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 previously published algorithm (Friston et al., 1996). Baseline drifts were corrected by high-pass filtering, implemented using a discrete Fourier transform with cutoff periods of 15 and 27 s in Experiments 1 and 2, respectively. In the spatial domain, the data were filtered using a Gaussian filter with
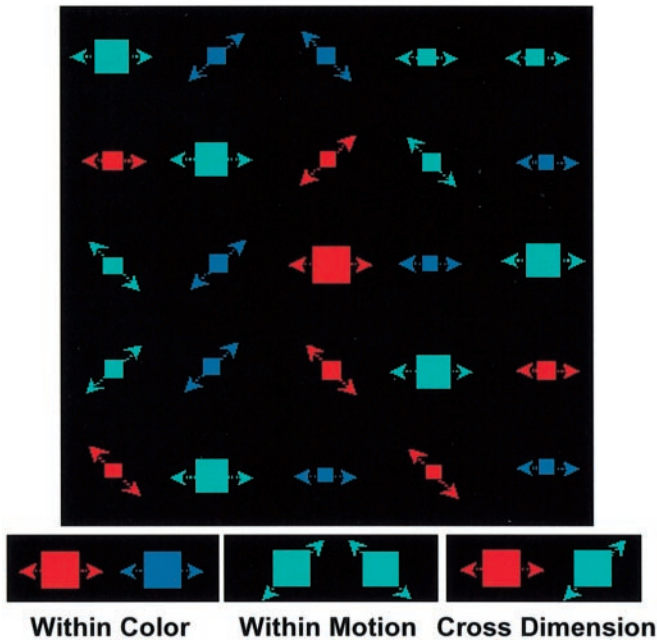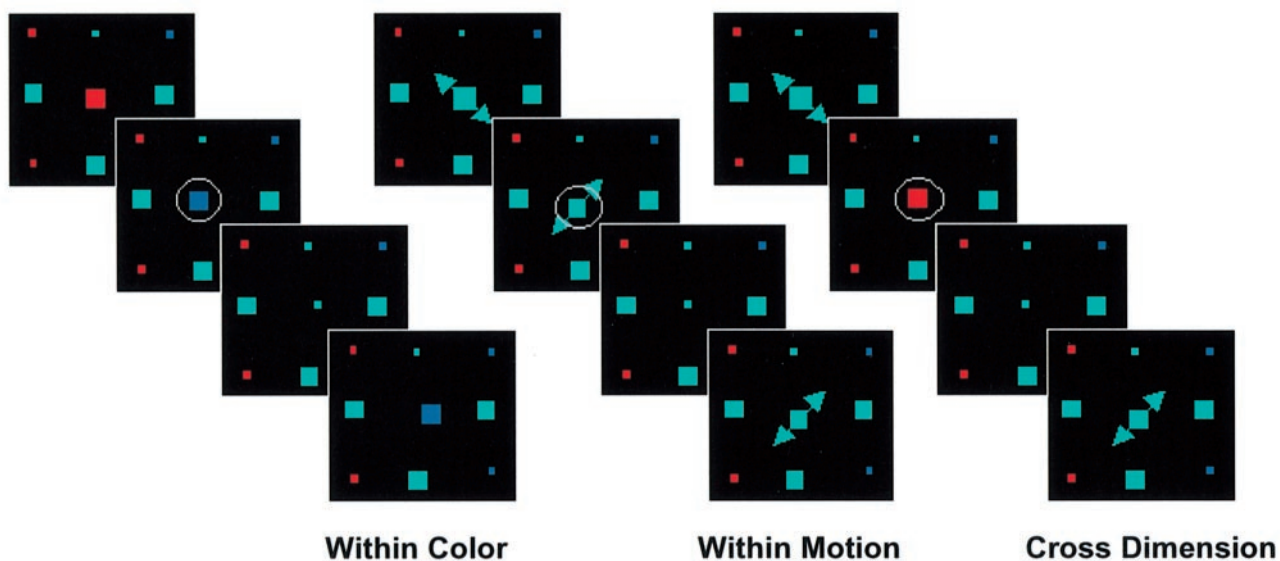

Figure 2. Illustration of the experimental design. The three different experimental conditions — within-color search (left), within-motion search (middle), cross-dimension search (right) — are depicted. The three experimental conditions differed only with regard to the potential target stimuli, but not in terms of the distractor sets. Four example displays for possible targets are shown for each condition. Targets on feature- and, respectively, dimension-change trials are marked by a white circle. All display items moved (see Fig. 1), but here only the motion direction of the motion-defined target is indicated by arrows.

FWHM = 7 mm. Following this preprocessing, the functional data sets were co-registered with the individual observers' high-resolution anatomical data sets and normalized by linear scaling. Data were analysed using the general linear model (Friston *et al.*, 1995). Event-related analyses were performed using a model of the hemodynamic response and its temporal derivative (Friston *et al.*, 1995; Josephs *et al.*, 1997). Group statistics were calculated by one-sample *t*-tests at corresponding voxels of the individual SPM{*z*} across observers (Bosch, 2000). The significance criterion was set to $\alpha = 0.0005$ (uncorrected) for whole-brain analyses.

For the presentation of unthresholded signal changes in specified areas, activated blobs were identified individually for each observer. For a given region of interest (ROI), the strongest activation was selected automatically within a 5 mm range from the location of the maximum group *z*-score. If this activation was located within the same anatomical structure as the maximum group *z*-score, the location was accepted for the extraction of signal change values. Otherwise, the location of the highest individual *z*-score within that anatomical structure (inside the 5 mm range) was selected manually. For the voxels thus identified, the averaged percentage signal changes were extracted for the different experimental conditions. The maximum signal change within a time window of 7 s from stimulus onset was selected. Mean percentage signal changes across all observers and the associated 95% confidence intervals (CI), corrected for inter-individual variances (Loftus and Masson, 1994), were calculated.

Results

Experiment 1

Experiment 1 was designed to reveal the functional neuro-anatomy of visual search for singleton conjunction targets, by comparing cross-dimensional search against within-dimensional search. Before presenting the functional-imaging data, the behavioral (RT) data will be considered.

Behavioral Data

Figure 3*a* presents the group mean correct RTs in the within- and cross-dimension search conditions, separately for target-present and target-absent trials. The data were examined by a two-way repeated-measures analysis of variance (ANOVA), with the factors search condition (within-dimension, cross-dimension) and target presence (present, absent). Target-absent RTs were overall slower than target-present RTs [main effect of target presence, $F(1,9) = 78.72$, $MS_e = 65\,720.19$, $P < 0.01$]. More importantly, RTs were overall slower in cross-dimension search than in within-dimension search [main effect of search condition, $F(1,9) = 37.953$, $MS_e = 11\,358.417$, $P < 0.01$]. This cross-dimension search cost was evident for target-present and absent RTs alike, though the cost was more marked for target-absent responses [interaction, $F(1,9) = 7.66$, $MS_e = 5642.70$, $P < 0.01$].

Figure 3*b* presents the group mean target-present RTs in the within- and cross-dimension conditions, separately for change trials and for no-change trials. The data were examined by a repeated-measures ANOVA with the factors search condition (within- versus cross-dimension) and target change (change, no-change). Cross-dimension search RTs were overall slower than within-dimension search RTs [main effects of search condition, $F(1,9) = 46.06$, $MS_e = 5613.07$, $P < 0.01$]. Furthermore, RTs were overall slower on change trials than on no-change trials [main effect of target change, $F(1,9) = 17.56$, $MS_e = 4235.60$, $P < 0.01$]. Importantly, however, the change effect was revealed to be dimension-specific [interaction, $F(1,9) = 10.85$, $MS_e = 4381.46$, $P < 0.01$]: changes in the target-defining dimension (cross-dimension search) led to significantly increased detection latencies relative to no-change trials [by 155 ms, on average; planned *t*-tests, $t(9) = 4.21$, $P < 0.01$], whereas feature
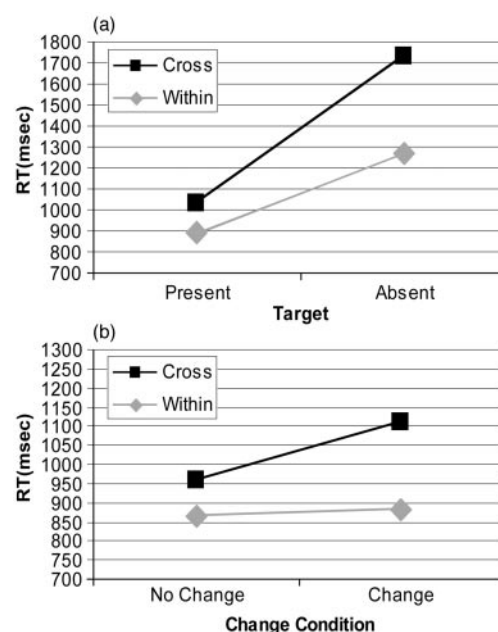

Figure 3. (*a*) Group mean reaction times for target-present and target-absent trials in within- and cross-dimension search. (*b*) Group mean reaction times for change and no-change trials in within- and cross-dimension search.

changes within a dimension (within-dimension search) did not [$t(9) = 0.90$, n.s.].

This pattern of RT effects, characterized by cross-dimension search cost and dimension-specific change effects, replicate those found previously (Müller *et al.*, 1995; Found and Müller, 1996) in singleton feature search tasks (Pollmann *et al.*, 2000). However, the effect sizes were greatly increased in the singleton conjunction search task observers had to perform in the present study. The cross-dimension search cost was increased from 26 ms (simple feature search) to 161 ms (conjunction search) and the dimensional change effect was increased from 48 to 155 ms [while the overall RTs were markedly slower for conjunction search relative to simple feature search: 873 ms versus 428 ms (within-dimension search] and 1033 ms versus 454 ms (cross-dimension search)]. To confirm that RT effects were not due to a speed–accuracy trade off, a repeated-measures ANOVA was calculated on the errors (cross-dimension change versus no-change, 7.1 versus 5.9%; within dimension change versus no-change, 3.1 versus 2.1 %). Neither the main effects for search-condition [$F(1,9) = 3.139$, n.s.] or change-condition [$F(1,9) = 0.007$, n.s.], nor their interaction [$F(1,9) = 2.250$, n.s.] were significant.

Functional-imaging Data

Activations Related to Visual Search. To assess activations related to visual search performance unaffected by dimensional-change processes, hemodynamic responses to target-present trials in within-dimension search were compared with the respective fixation periods following each block. This analysis revealed activations in the frontomedian wall (BA 32/6) at the putative location of the human pre-supplementary eye field (Petit *et al.*, 1996) and, bilaterally, at the junction of the superior precentral and superior frontal sulci, the location of the human frontal eye field (Paus, 1996; Luna *et al.*, 1998). The anterior insula was activated in the right hemisphere. Posterior parietal activation was found bilaterally along the posterior intraparietal

Table 1

Activations related to target-present trials in within-dimension search compared to fixation

Structure	Group Z_{max}	Location
Medial surface/superior frontal gyrus BA 32/6	5.565	R (4, 10, 43)
Superior precentral sulcus/FEF BA 6	6.04	R (28, –6, 41)
	6.869	L (–29, –7, 38)
Intraparietal sulcus (horizontal leg) BA 7	9.913	L (–22, –57, 46)
	9.993	R (23, –57, 46)
Superior postcentral sulcus BA 40/2	8.231	L (–37, –37, 39)
	5.789	R (40, –38, 36)
Superior precentral gyrus BA 6	6.844	R (40, 3, 27)
Anterior insula	4.54	R (31, 17, 9)
Middle occipital gyrus BA 19	10.008	L (–22, –95, 16)
	10.304	R (41, –66, 7)
	10.714	L (–37, –75, 9)
	12.27	R (19, –96, 13)
Inferior cuneus BA 18	12.801	L (–8, –103, 6)
Calcarine sulcus BA 17	13.528	R (14, –86, 0)
Lingual gyrus BA 18	13.338	L (–16, –85, –9)
Cerebellum	6.029	R (2, –77, –25)
	4.221	R (20, –69, –32)

Coordinates indicate the peak activation in the coordinate system of Talairach and Tournoux (Talairach and Tournoux, 1988).

Table 2

Activations related to the interaction of search condition (within-, cross-dimension) × change condition (change, no change)

Structure	Group Z_{max}	Location
Superior frontal gyrus (dorsal margin) BA 8	3.83	R (17, 11, 49)
Superior frontal sulcus (anterior division) BA 9/10	4.87	R (14, 49, 26)
Pregenual anterior cingulate BA 32 (medial frontal wall)	3.96	R (8, 43, 1)
	4.1	L (–14, 47, 3)
Superior frontal gyrus (medial surface) BA 8	3.8	R (5, 34, 44)
Superior frontal gyrus (medial surface)/ACC BA 8/32	4.07	R (5, 34, 26)
Posterior cingulate BA 23	3.7	L (–8, –44, 26)
Superior temporal gyrus (posterior division) BA 41	3.91	R (47, –27, 5)
Middle temporal gyrus (posterior division) BA 22	3.97	R (53, –43, 2)
Caudate	3.48	L (–2, 9, 0)
	3.65	L (–14, 20, –5)
Putamen	3.68	R (23, 19, –8)

Coordinates indicate the peak activation in the coordinate system of Talairach and Tournoux (Talairach and Tournoux, 1988).

sulcus (IPS) and, more anteriorly, in the superior postcentral sulci (BA 40/2). In occipital cortex, there was widespread bilateral activation of visual processing areas (BA 17–19; see Table 1).

Dimensional Inter-trial Effects. To examine activation changes associated with dimensional inter-trial effects, an event-related analysis was carried out across the within- and cross-dimension search conditions. All trials in the within-dimension conditions on which the target feature in the second target-defining dimension was different from that on the preceding trial were marked as feature-change trials, and trials on which the feature remained the same were marked as feature-no-change trials. Likewise, all trials in the cross-dimension condition on which the second target-defining dimension was different from that on the preceding trial were labeled as dimension-change trials, and trials on which the dimension stayed the same were labeled as dimension-no-change trials (Fig. 2).

In order to assess which brain areas are specifically involved in dimension changes, beyond general change-related activation which may also be elicited by featural change, the interaction of the factors search condition and target change [i.e. (cross-dimensional change – no-change) – (within-dimensional change – no-change)] was examined. This interaction was revealed to be significant in several locations in right superior frontal gyrus, the most posterior covering its medial surface extending in an anterior and lateral direction across its superior margin into the anterior third of the superior frontal sulcus (SFS; see Table 2 and Fig. 4). The interaction was significant in the dorsal and medial division of the right superior frontal gyrus, as well as bilaterally in a cortical area around the pregenal portion of the cingulate sulcus (BA 32/24) and in the left posterior cingulate (BA 23). Furthermore, the interaction was significant in the posterior division of the right superior and middle temporal gyri. Subcortical activation was observed in the left caudate nucleus and putamen.

Since we observed dimensional change-related activation in left lateral frontopolar cortex in our study of pop-out search (Pollmann *et al.*, 2000), we carried out an ROI analysis at this location. At the lowered threshold of α = 0.001 (uncorrected),

we found significant frontopolar activation (Z_{max} = 3.24, x = –20, y = 47, z = 5).

The above analysis is ambivalent as to the source of the interactions. Interactions may be significant in areas that are selectively activated by dimension changes, but not by feature changes. However, significant interactions may also result from selective signal decreases related to feature changes. Therefore, to determine more precisely the source of the interactions, event-related analyses were carried out for each of the two search conditions separately.

Activations Related to Dimensional Change. An event-related analysis was calculated comparing change versus no-change trials in cross-dimension search. Of the brain areas that exhibited significant activations in the interaction analysis, the cortex along the banks of the anterior right SFS was activated, along with the pregenual ACC and the posterior cingulate/precuneal area bilaterally (see Table 3 and Fig. 5). Additional activations, that were not significant in the interaction analysis, were observed in left precuneus and in left posterior intraparietal sulcus, extending into superior parietal lobule

Dimension-change-related activation was found in lateral and medial occipital cortex. Activation in lateral occipital gyrus was observed bilaterally within the probability map border of V5, as described previously (Hasnain *et al.*, 1998). The location of activation in left fusiform gyrus matched the coordinates given for areas V4a (Bartels and Zeki, 2000).

Activations Related to Featural Change. An event-related analysis comparing change versus no-change trials in within-dimension search blocks revealed only one focus of significant activation change in the posterior division of the right cuneus (BA 18; Z_{max} = 3.64, x = 8, y = –98, z = 14). The scarcity of activation changes related to feature change is consistent with the absence of behavioral feature change costs.

Signal Changes Related to Feature and Dimension Changes. To examine whether the differences between dimension and feature changes were qualitative rather than quantitative in nature, we analysed the unthresholded signal changes for all conditions, averaged across all observers, in several ROIs (Fig. 6).

In left pregenual ACC, this analysis revealed a distinct dimensional change-related activation pattern. Changes of the target-defining dimension resulted in a signal increase compared to

non-changes in cross-dimension search [planned *t*-test, *t*(9) = 3.56, *P* < 0.01]. In contrast, feature changes did not lead to differences relative to non-changes in within-dimension search [planned *t*-test, *t*(9) = 0.76, n.s.].

In left frontopolar cortex, no significant differences were obtained for either dimension changes [cross-dimension search; planned *t*-test, *t*(9) = 1.13, n.s.] or feature changes [within-dimension search; planned *t*-test, *t*(9) = 0.99, n.s.]. Compared to ACC, any dimensional change-related signal increase was reduced and signal variability was increased (Fig. 6).

The comparison of dimensional change versus no-change (cross-dimension search) revealed an activation in IPS that had not been apparent in the initial (search condition × target change) interaction analysis. IPS activation was significantly increased following changes in the target-defining dimension [planned *t*-test, *t*(9) = 3.87, *P* > 0.01], while also showing some increase following within-dimension feature changes [planned *t*-test, *t*(9) = 2.32, *P* > 0.05]. This weak signal increase accounts for the absence of a significant interaction.

Experiment 2

After establishing the network involved in top-down controlled dimension changes in Experiment 1, stimulus-driven and top-down controlled dimension changes were directly compared in Experiment 2. Observers performed both a singleton conjunction search task, which was identical to the cross-dimensional condition of Experiment 1, and a singleton feature task, in which targets were defined by a simple feature contrast in one of the two alternative dimensions. Differences in frontal activation were expected to be observed in pregenual ACC and left lateral frontopolar cortex. Pregenual ACC was expected to be more strongly involved in top-down controlled dimension changes and left lateral frontopolar cortex was expected to show stronger activations related to stimulus-driven dimension changes.
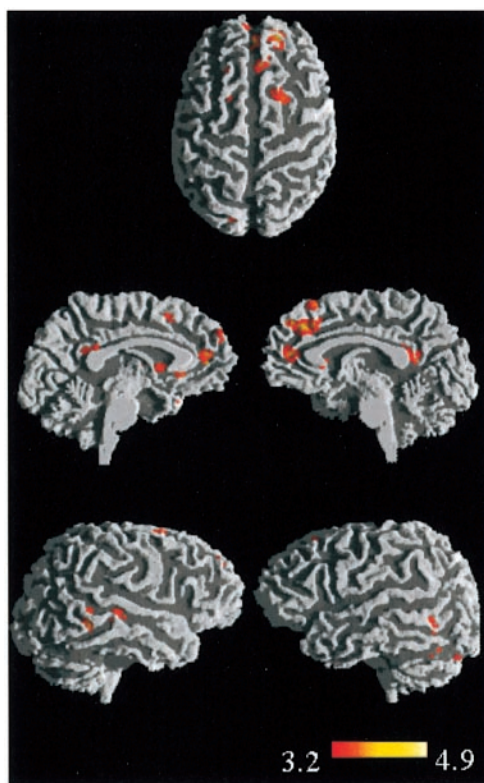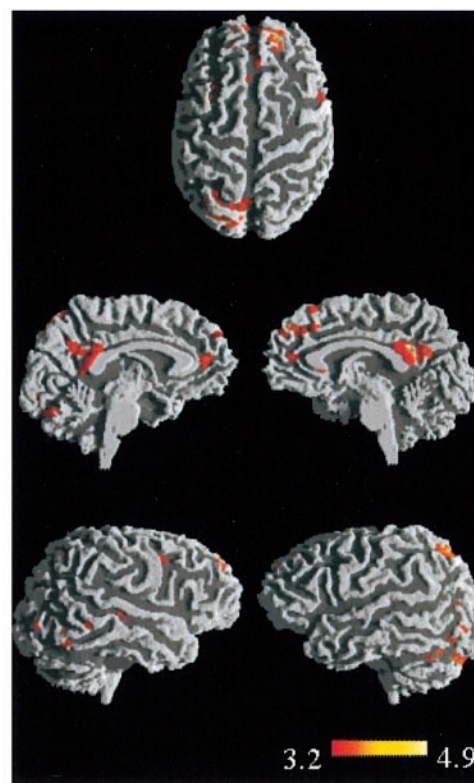
Table 3
Activations related to changes in cross-dimension search compared to no-changes

Structure	Group Z_{max}	Location
Superior frontal gyrus (dorsal margin) BA 10	3.53	L (–11, 56, 19)
Superior frontal sulcus (anterior division) BA 9	4.48	R (14, 52, 25)
Pregenual ACC (medial frontal wall)	3.82	L (–10, 47, 3)
	3.66	R (10, 43, 1)
Superior frontal gyrus (medial surface) BA 32/9	3.56	R (4, 34, 29)
Posterior cingulate/inferior precuneus BA 23	3.95	R (10, –46, 26)
Posterior cingulate BA 23	3.47	L (–8, –49, 27)
	3.47	L (–4, –52, 16)
Superior /anterior precuneus	3.61	L (–5, –58, 57)
Intraparietal sulcus (horizontal leg) BA 7	4.24	L (–14, –71, 52)
Fusiform gyrus BA 37	3.73	L (–26, –58, –12)
Lingual gyrus BA 18	3.93	L (–13, –83, –12)
Lateral occipital gyrus (inferior division) BA 19	3.54	R (44, –63, –5)
Lateral occipital gyrus BA 18	3.64	L (–40, –65, –13)
Lateral occipital gyrus (superior division) BA 18	4.05	L (–17, –94, 7)
Lateral occipital gyrus (superior division) BA 19	3.65	L (–37, –76, 4)

Coordinates indicate the peak activation in the coordinate system of Talairach and Tournoux (Talairach and Tournoux, 1988).

Figure 4

Figure 5

Figure 4. Brain areas exhibiting significant interaction of search condition (within-, cross-dimension) × change condition (change, no change), projected onto a surface rendering of an individual brain.

Figure 5. Brain areas exhibiting increased activation on change trials compared with no-change trials in cross-dimension search.
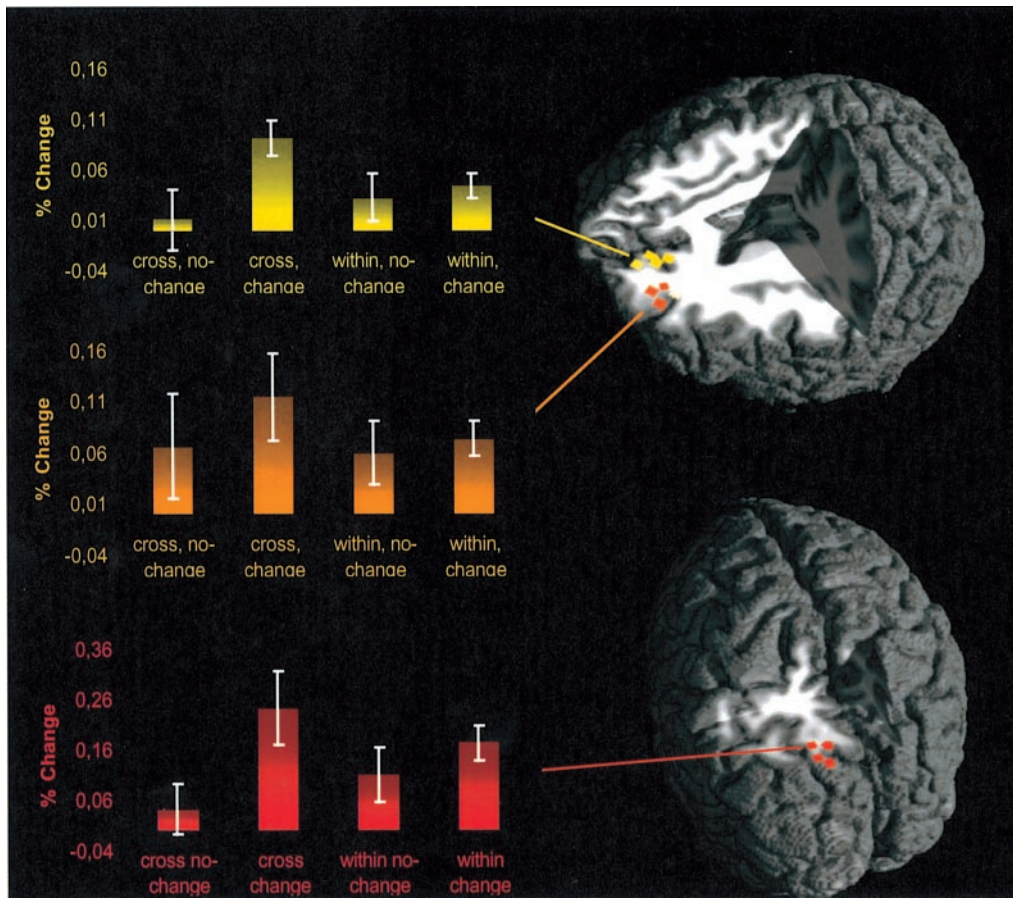
Figure 6. Percentage signal change in ROIs for each combination of search (within-, cross-dimension) and change (change, no change) condition, averaged over 10 observers (the figure shows only the subset of locations of individual peak activation lying in the viewing plane). Error bars indicate 95% confidence intervals (CI), corrected for inter-individual differences (Loftus and Masson, 1994). Left pregenual ACC (top/yellow) showed a clear difference between dimensional-change and no-change trials. In lateral prefrontal cortex, there were no clear effects of dimensional changes versus no-changes (middle/orange). Signal changes in IPS showed effects related to visual dimension changes, but no reliable effects related to feature changes within a dimension (bottom/red).

Behavioral Data

Figure 7 presents the group mean RTs for the feature and conjunction search tasks of Experiment 2, separately for dimension change and no-change trials. A two-way repeated-measures ANOVA with the factors search task (feature, conjunction) and target change (change, no change) revealed all effects to be significant. Conjunction search was overall slower than feature search [main effect of search condition, $F(1,7) = 76.2$, $MS_e = 11\,515.3$, $P < 0.01$]. RTs were slower on dimension change trials than on no-change trials [main effect of target change, $F(1,7) = 26.41$, $MS_e = 2244.0$, $P < 0.01$], and the change effect differed between the two conditions [interaction, $F(1,7) = 11.83$, $MS_e = 9181.43$, $P < 0.05$]: it was increased in the conjunction search task relative to the feature search task, consistent with the present Experiment 1 and previous results (Pollmann *et al.*, 2000).

Functional-imaging Data

Signal Changes Related to Top-down versus Bottom-up Controlled Dimension Changes. In order to evaluate the role of prefrontal cortex during internally and externally controlled dimension changes, an event-related analysis was carried out across the feature and conjunction search tasks. The interaction of the factors search task and target change, i.e. ((conjunction change – no-change) – conjunction null-events) – ((pop-out
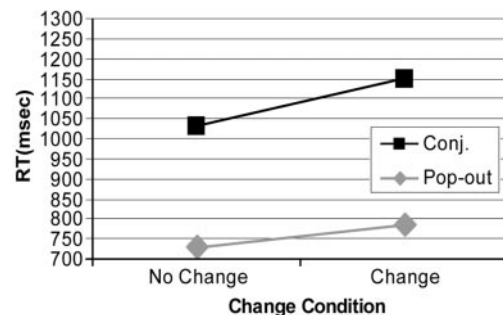

Figure 7. Group mean reaction times for change and no-change trials in the singleton feature and singleton conjunction search tasks.

change – no-change) – pop-out null-events)), was examined. This analysis revealed a significant interaction in pregenual ACC ($Z_{max} = 3.4$, $x = -8$, $y = 48$, $z = 6$) and a marginally significant interaction in left lateral frontopolar cortex ($Z_{max} = -2.9$, $x = -29$, $y = 47$, $z = 3$). Unthresholded signal changes in two ROIs at these locations were analysed for all conditions of Experiment 2. Differential activation pattern were observed in pregenual ACC and frontopolar cortex (see Fig. 8 for the results averaged across all observers).

In left pregenual ACC, changes of the target-defining dimension resulted in a stronger signal increase compared to no-
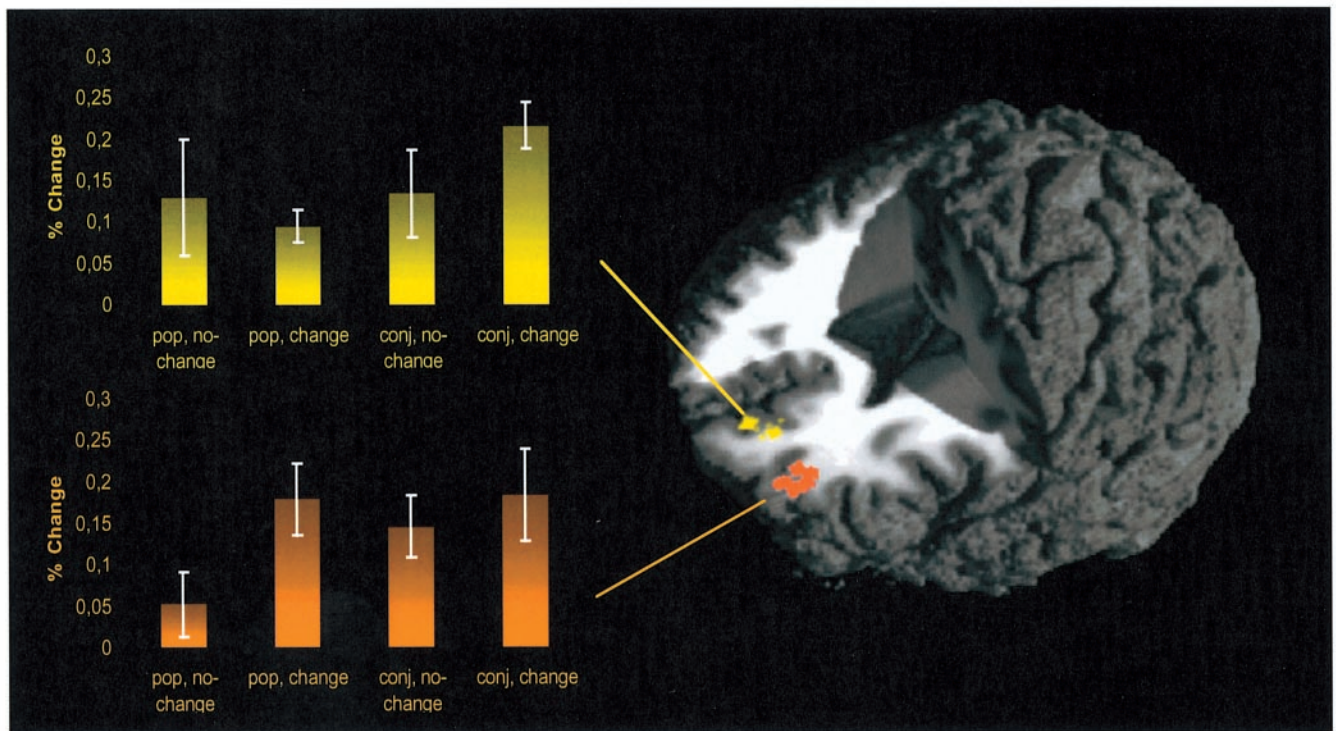
Figure 8. Percentage signal change in ROIs in left lateral frontopolar cortex and in left pregenual ACC, averaged over eight observers (the figure displays only the subset of locations of individual peak activation lying in the viewing plane). Error bars indicate 95% confidence intervals (CI), corrected for inter-individual differences (Loftus and Masson, 1994). Left pregenual ACC showed a clear difference between dimensional change and no-change trials in the conjunction search task, but not in the feature search task (top/yellow). In lateral prefrontal cortex, differences between change and no-change trials were only observed for the feature search task (bottom/orange).

change trials only in the complex singleton conjunction search task [planned t-tests, $t(7) = 4.09$, $P < 0.05$], but not in the simpler singleton feature task [planned t-tests, $t(7) = -0.95$, n.s.].

Exactly the reverse pattern was manifest in left frontopolar cortex. In the conjunction search task, no significant difference in signal change was obtained for dimension change relative to no-change trials [planned t-tests, $t(7) = 0.82$, n.s.]. In contrast, in the feature search task, changes in the target dimension produced a strong signal increase compared to no-change trials [planned t-tests, $t(7) = 3.26$, $P < 0.05$].

Discussion

Behavioral Data
The behavioral data of Experiment 1 revealed clear effects of switching between visual dimensions, more precisely between secondary target-defining dimensions, in singleton conjunction search. Target detection RTs were much slower overall in cross-dimension search (in which dimension switching was necessary) than in within-dimension search (in which there were no dimension switches). Furthermore, in cross-dimension search, RTs were markedly slower on switch trials than on no-switch trials (while there were no feature switch effects in within-dimension search). This pattern of results parallels the findings with singleton feature search (Müller *et al.*, 1995; Found and Müller, 1996; Pollmann *et al.*, 2000). Thus, it is safe to conclude that the notion of dimensional weighting does extend to singleton conjunction search.

Direct comparison of conjunction and feature searches in Experiment 2 revealed detection RTs to be significantly slowed for singleton conjunction targets relative to singleton feature targets. Furthermore, while significant RT costs associated with

dimensional change were evident in both tasks, the change effect was significantly stronger in singleton conjunction search compared to singleton feature search. This pattern essentially replicated the present Experiment 1 and previous findings (Pollmann *et al.*, 2000) within a single experiment.

We propose that the slow RTs in singleton conjunction search reflect two successive processing stages: the first being a filtering stage (Kahneman and Treisman, 1984) selecting items by their (large) size, the primary target-defining dimension, and the second involving search within or across the secondary target-defining dimension(s) of the items selected in the first stage. Size-based filtering might work by weighting the size dimension, so that there would be less attentional weight available for processing the secondary dimension. This would have two consequences: First, it would take longer to ascertain whether or not a (target) saliency signal is present in the secondary dimension. Second, in cross-dimension search, if there is no saliency signal in the secondary dimension checked first, switching over to the alternative secondary dimension would be correspondingly delayed and, again, it would take longer to ascertain whether or not a saliency signal is present in this dimension. Thus, the need for a filtering stage would explain why target detection RTs are generally slower in singleton conjunction search than in singleton feature search (even for within-dimension search). The reduced attentional weight available to be allocated to any secondary target-defining dimension could explain why the dimension switch costs are increased in singleton conjunction relative to singleton feature search.

An alternative possibility is that size is not an independent dimension, but nested within the color and motion dimensions. As a result, size-based filtering would have to be implemented within each dimension separately. Consequently, as in the

scenario sketched above, a filtering process within each 'secondary' dimension would have to precede the computation of feature differences amongst the relevant items. However, unlike the above scenario, when search involves switching between dimensions, the filtering process would have to be carried out anew for the secondary dimension checked second. This would also produce a marked increase in switch costs relative to simple singleton feature search in which no filtering is required.

In any case, linked processing of multi-dimensional stimulus information and/or switching between 'linkages' (size and color, size and motion) are likely to be operations demanding a high degree of top-down control. Thus, while dimension switches in singleton feature search might be effected relatively automatically, without top-down intervention (once the basic processing parameters are set), dimension switching in singleton conjunction search is more likely to involve ongoing top-down intervention, accounting for the increased switch costs.

Functional Imaging Data: Dimensional Change Network

Two Distinct Networks
The analysis of the fMRI data of Experiment 1 revealed two distinct networks of brain structures, one supporting visual search in general and the other involved in visual dimension switching in cross-dimensional conjunction search. The first network, which had previously been shown to be active during visuo-spatial orienting and visual search (Corbetta, 1998; Pollmann and von Cramon, 2000), consisted mainly of the frontal and supplementary eye fields, bilateral postcentral and posterior intraparietal sulcus, and widespread activation in visual cortical areas. In contrast, structures uniquely involved in visual dimension switching (analysed by the interaction of search and change conditions) were found in the dorsal and medial right superior frontal gyrus and in several locations in cingulate gyrus.

Those areas within the visual search network that exhibited increased activation with dimensional change, such as the left posterior IPS and bilateral spots of activation in lateral occipital cortex at the probable location of V5, were involved in more general change-related processes, as indicated by the absence of a significant search condition × change interaction.

Dimensional Change-related Activation in Frontal Cortex
Our previous singleton feature search study (Pollmann et al., 2000) revealed changes of the target-defining dimension to be associated with left frontopolar activation. In the present Experiment 1, in which observers had to perform a more complex singleton conjunction search, dimension changes activated parts of the anterior frontomedian wall along the pregenual portion of the cingulate sulcus (BA 32/24) bilaterally.

Since the fundus of lateral frontopolar cortex is in the close vicinity of this anterior frontomedian area, we carefully extracted, individually for each observer, the location of maximum dimensional change-related activation in frontopolar and anterior frontomedian cortices. Signal amplitudes at these locations showed a clear distinction: activation was significantly increased following top-down controlled visual dimension changes in the anterior frontomedian wall along the pregenual cingulate sulcus (BA 32/24), but not in frontopolar cortex. Although there was some tendency towards a dimensional change-related signal increase in frontopolar cortex, it was much smaller than that in anterior frontomedian cortex (while also exhibiting higher signal variability). This contrasts with our previous data on stimulus-driven dimension changes in singleton

feature (pop-out) search. Stimulus-driven dimensional change-related activation, although observed both in frontopolar and frontomedian cortices, was much larger in lateral frontopolar cortex (Pollmann et al., 2000); see Figures 3 and 4.

This differential effect between singleton conjunction and singleton feature search was confirmed in Experiment 2, which permitted the roles of the left pregenual ACC and left frontopolar cortex in the two tasks to be compared directly within the same observers. For each observer, the locations with the highest activation indicative of a change condition × search task interaction were extracted in left pregenual ACC and left lateral frontopolar cortex, respectively. Differential signal change patterns were revealed between the two tasks: for singleton feature search, a difference between dimension change and no-change trials was evident in lateral frontopolar cortex; in contrast, for the singleton conjunction task, a difference was manifest in pregenual ACC (Fig. 8).

For singleton feature search, dimension changes elicited a strong response in lateral frontopolar cortex, whereas no changes were associated with a weaker signal change. Target detection in singleton feature search is based on a salient feature difference in a single (primary) dimension, which, on change trials, may attract attentional weight to the new dimension in a largely stimulus-driven manner (Müller et al., 1995). Lateral frontopolar cortex seems to be exclusively involved in this process of switching from one (primary) visual dimension to another.

A more detailed analysis showed that frontopolar activation was comparably increased for both change and no-change trials in singleton conjunction search and for dimension changes in singleton feature search (Fig. 8). In singleton conjunction search, targets were defined by a combination of features in a primary and a secondary dimension. During a given singleton conjunction search trial, attentional weight may be more strongly allocated first to the primary dimension – size – and subsequently to the secondary dimension – color or motion – implementing a sequential filtering operation (filtering by size followed by filtering by color or motion). As long as the filter parameters are set (e.g. size first, color second), this process may be performed automatically. But when the filter algorithm needs to be changed (i.e. when the parameters used on the previous trial do not lead to the detection of a target), top-down control must intervene to reset the parameters (e.g. size first, motion second). Consequently, while the automatic process (of switching from the first to the secondary dimension) would be involved in dimension change as well as no-change trials, the top-down process would be required only on change trials. Functionally, the automatic component in singleton conjunction search is similar to that of switching between primary dimensions in singleton feature search (Pollmann et al., 2000) and may therefore be supported by the same frontopolar mechanisms. This would explain the identical signal changes on dimension-change trials in feature search and change and no-change trials in conjunction search in lateral frontopolar cortex (Fig. 8). In contrast, the top-down controlled component is required only on secondary-dimension-change trials in singleton conjunction search and it involves mechanisms in frontomedian cortex.

Dimensional Change-related Activation in Posterior Cortex
An increased activation in cross-dimensional search (in the comparison of dimensional change versus no-change trials) was also found in left posterior IPS, extending into superior parietal lobule. However, this area did not show a significant change × search type interaction. Analysis of signal changes in left

posterior IPS showed a clear distinction between change and no-change trials in the cross-dimension search condition (Fig. 6). However, there was also a tendency towards increased feature-change-related activation in within-dimension search, which explains the non-significant interaction. Thus, IPS showed a general change-related activation not restricted to dimensional change.

Specific dimension change-related activation was further observed in right superior temporal gyrus and posterior cingulate cortex. These posterior brain areas may represent an intermediary stage between frontal areas involved in the control of dimension weighting and occipital dimension-specific visual cortices.

Endogenous versus Exogenous Switching Processes in Anterior Prefrontal Cortex

It has been proposed (Koechlin *et al.*, 2000) that the medial and lateral anterior prefrontal cortices support different aspects of task control. In a variant of the task-switching paradigm, they observed frontomedian wall activation (BA 10/32) comparable to that seen here when the switches occurred at predictable intervals, whereas lateral frontopolar activation was observed when the switch was unpredictable. This was interpreted as frontopolar involvement in exogenous (stimulus-driven) task switches versus anterior frontomedian involvement in endogenous (top-down controlled) switches. Our experiments differed from that of Koechlin *et al.* in several important respects. First, we investigated attentional switching between visual dimensions, rather than task switching. Second, dimensional change was always unpredictable. Nevertheless, our data support the distinction between frontopolar support of exogenous and frontomedian support of endogenous processes.

Recently, a left frontopolar activation at the same location as in the present experiments was observed in a study from our laboratory (Lepsien and Pollmann, 2002) when subjects had to redirect attention away from exogenous spatial cues. As in the singleton feature search experiments – our Experiment 2 and Pollmann *et al.* (Pollmann *et al.*, 2000) – left frontopolar activation was observed in the spatial cueing experiment when attention had to be reallocated against stimulus-driven attentional capture.

Further support for an exogenous/endogenous processing distinction in anterior prefrontal cortex comes from a recent study (Rogers *et al.*, 2000), which compared dimension changes ('extradimensional shifts') in the Wisconsin Card Sorting Test (WCST) with feature changes within a given dimension ('intra-dimensional shifts'). Rogers *et al.* reasoned that prefrontal cortex is involved in initiating processes of overriding acquired attentional sets. The comparison of extradimensional and intradimensional shifts revealed an anterior frontomedian activation (BA 10), but no lateral frontopolar activation, in line with the proposal that anterior frontomedian structures are involved in endogenous shifts. Furthermore, they found an activation very close to our anterior superior frontal sulcus (BA9) activation, which was related specifically to dimensional change. Our singleton conjunction search experiment shares with the WCST the demand for the establishment of a specific task set (filtering by size and search for either a color- or a motion-defined feature difference) and the need to override this set when attention must be shifted to a new dimension. In contrast, in singleton feature search, there is less or no need for top-down control, and no SFS activation was observed.

In more general terms, we propose that the frontomedian wall has a function in the self-initiation of cognitive processes; that is, in the present case, endogenous shifts of attention to a new visual dimension. This is in line with the clinical observation that lesions restricted to the frontomedian wall (e.g. those caused by anterior cerebral artery infarction) produce a substantial reduction of self-initiated cognitive processes, ranging to apathy in extreme cases.

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