

Anterior Prefrontal Cortex Contributions to Attention Control

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Abstract. In a series of event-related functional magnetic resonance studies, we consistently found activation in anterior prefrontal cortex related to visual dimension changes in singleton search tasks. I review these data and discuss possible contributions of anterior prefrontal cortex to attention control in visual search. It is proposed that anterior prefrontal cortex may detect task-relevant stimulus changes when the target is ambiguously defined. This process may occur in the absence of awareness and may support visual dimension weighting by inhibition of the old relevant dimension in favor of the new dimension.

Key words: attention, working memory, executive processes, frontopolar cortex, fMRI

Introduction

Imaging studies of working memory and executive functions have consistently reported prefrontal activation. While the activation sites within the prefrontal cortex vary depending on the task employed, the large majority of activated areas belong to the lateral prefrontal cortex, roughly corresponding to Brodmann areas (BA) 46 and 9 dorsally, and BA 44 and 45 ventrally, and more posteriorly to the premotor cortex (see Figure 1). In contrast, the most anterior part of the prefrontal cortex, corresponding mainly to Brodmann area 10, is not typically activated in these studies (D'Esposito et al., 1998, Smith & Jonides, 1999).

As in the case of executive function, there is good agreement that posterior frontal areas support shifts of covert visuospatial attention. Specifically, the human frontal eye fields (FEF) and the supplementary eye fields (SEF) have consistently been found activated by covert attention shifts as well as overt saccades. But again, anterior prefrontal activation was not commonly seen in studies of covert or overt attention shifts (e.g., Corbetta et al., 1998, Gitelman et al., 1999) or visual search (Pollmann & von Cramon, 2000).

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In recent years, however, the interest in the functions supported by the anterior prefrontal cortex has increased. A number of studies have suggested that an area around the frontal poles, bordering ventrally on orbitofrontal cortex and including laterally roughly the anterior third of the frontal gyri and medially the frontomedian cortex anterior to the cingulate cortex, may be involved in cognitive control processes on a more abstract level than the executive processes supported by the more posterior dorso- and ventrolateral PFC. In this paper, I relate these data to our own finding of frontopolar involvement in attentional changes between visual dimensions and locations. I start with an overview of our findings and will then attempt to integrate these findings with emerging concepts of anterior prefrontal function. It is not the aim of this paper to review the cognitive neuroscience literature related to anterior prefrontal cortex. For alternative concepts of anterior prefrontal function, the reader is referred to Christoff and Gabrieli (2000), Christoff et al. (2001), and Koechlin, Basso, Pietrini, Panzer, and Grafman (1999).

Frontopolar Involvement in Visual Dimension Changes

In a series of event-related functional magnetic resonance imaging (fMRI) studies, my colleagues and I have investigated the neural basis of attentional

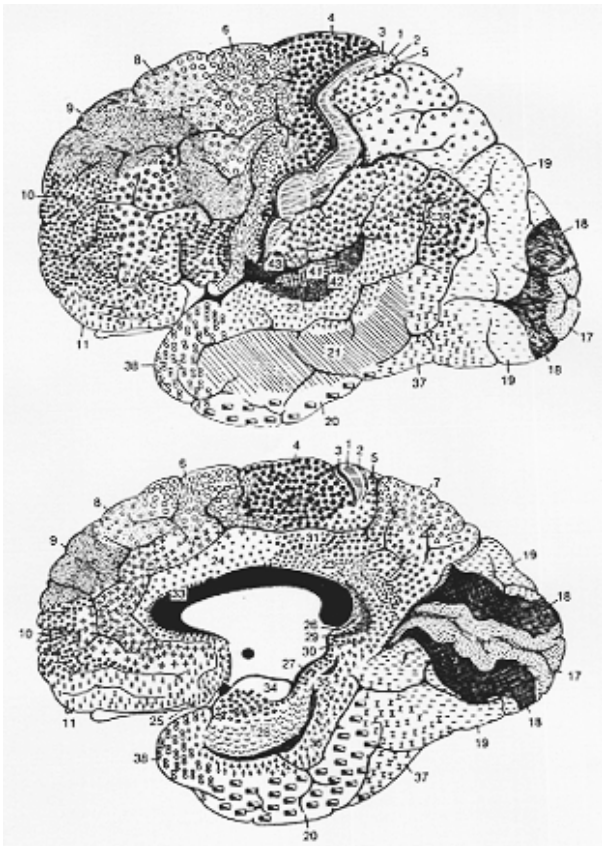


Figure 1. Cytoarchitectonic areas after Brodmann (1909).

changes between visual dimensions. The basic paradigm used in these studies was visual search for singleton targets. Singleton, or odd-one-out targets, are defined by their uniqueness in a display filled with distractor items. In a display of green, horizontally moving items, for example, singletons may be a single red item or a single green item moving in an oblique direction. These were in fact the stimuli we used in our first fMRI study.

In visual search for singleton 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 color-defined target following a motion-defined target; Found & Müller, 1996). In contrast, no such change costs are observed when the target is defined by a different feature within the same visual 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 resources are allocated to the target-defining dimension to amplify the target’s saliency signal generated within this dimension. In the case of salient targets, characterized by a deviant single feature, as described above, allocation of attention to the target-defining dimension is largely stimulus-driven. Dimension changes incur a cost because attentional weight is shifted from the old to the new dimension.

In a first event-related fMRI study, we have investigated the neural network underlying these stimulus-driven attentional dimension-weighting processes. We identified an extended fronto-posterior network that was physically activated when the target-defining dimension changed across trials (Pollmann, Weidner, Müller, & von Cramon, 2000). This network consists of multiple posterior visual brain areas – including fusiform gyrus, lateral occipital gyrus, superior temporal sulcus and middle temporal gyrus, superior parietal lobule and precuneus – that are known to be involved in the attentional modulation of visual processing. In addition, we found a strong anterior prefrontal activation in the left frontopolar cortex and a weaker activation in the anterior frontomedian cortex, at the anterior border of the pregenual anterior cingulate gyrus.

Stimulus-Driven Versus Top-Down Controlled Changes

While singleton feature search may proceed rather automatically, top-down control processes 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). In two further event-related fMRI experiments, we (1) investigated the neural basis of top-down controlled visual dimension changes in a singleton conjunction search task and (2) directly compared the change-related activation elicited by stimulus-driven and top down-controlled visual dimension changes in the same subjects (Weidner, Pollmann, Müller, & von Cramon, 2002).

The singleton conjunction search task required observers to detect a target defined by a conjunction of size and either color or motion. In cross-dimension singleton conjunction search, the target was defined, unpredictably on a given trial, either by a unique combination of size with color (the only *large red* target) or a unique combination of size with motion (the only *large* target oscillating in the *lower right-upper left* direction).

The main issue of interest 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. Our previous singleton feature search study (Pollmann et al., 2000) had revealed changes of the target-defining dimension to be associated with left frontopolar activation. This activation was not observed in singleton conjunction search; instead, dimension changes activated parts of the anterior frontomedian wall along the pregenual portion of the cingulate sulcus. This differential effect between singleton conjunction and singleton feature search was confirmed in a further experiment, which permitted the roles of the left pregenual frontomedian cortex and the left frontopolar cortex in the two tasks to be compared directly within the same observers. Differential signal change patterns were revealed between the two tasks: for the singleton feature task, a dimension change-related signal increase was only evident in the lateral frontopolar cortex; in contrast, for the singleton conjunction task, a difference was manifest only in the pregenual frontomedian cortex (Figure 2).

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 (see Müller et al., 1995). The lateral frontopolar cortex seemed to be involved in this process of switching from one (primary) visual dimension to another, although the precise nature of its involvement was yet to be investigated.

In the remaining sections of the paper, I concentrate on the role of the lateral frontopolar cortex in

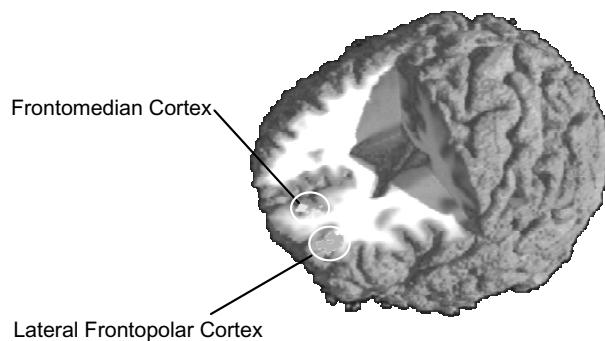


Figure 2. Anterior prefrontal loci of activation related to stimulus-driven and top-down controlled visual dimension changes. Lateral frontopolar activations showed a dimension-change-related increase selectively for stimulus-driven visual dimension weighting, whereas frontomedian activations selectively increased with top-down controlled visual dimension changes. (Figure adapted from Weidner et al., 2002, Figure 8.)

the control of attention. We carried out a further experiment to ensure that the dimension-change-related left frontopolar activation indeed indicated an involvement of this structure in the reallocation of attention, and whether this function is specific to changes of attention.

Stimulus Versus Response Changes

In a recent event-related fMRI study with normal subjects, we investigated the specificity of the dimension-weighting network by comparing stimulus-driven visual dimension changes with response changes (Pollmann, Weidner, Müller, & von Cramon, 2004). We expected that visual dimension changes would be associated with stronger activation changes in posterior visual brain areas, while response changes would be associated with increased activation in the motor and premotor cortices. More importantly, however, this study asked whether prefrontal areas (in particular, the left lateral frontopolar cortex) are specifically involved in visual dimension changes, as opposed to response changes. To investigate these issues, we employed a visual singleton search paradigm using a “compound” task, in which the target (a triangle stimulus pointing left or right) was characterized by a salient feature in one of two possible dimensions, color or motion, whereas the response to be made to the target was governed by its pointing direction, left or right. Thus, target detection depended on finding a salient color or, respectively, motion feature. In contrast, the response was governed by the pointing direction of the target triangle: if it pointed to the left, the left of two buttons had to be pressed; if it pointed to the right, the right button had to be pressed. The nontarget triangles pointed randomly to the left and right. Changes in the target-defining visual dimension across trials, such as from color to motion (as in the above example), occurred orthogonal to changes in the required response.

As expected, dimension changes led to phasically increased activation in posterior brain areas involved in visual processing. Response changes, by contrast, led to increased activation in the motor-related area, including the hand motor area of the left hemisphere, contralateral to the response hand. While these findings were not surprising given the nature of the changes, the more interesting question concerned the functional specificity of the frontal areas involved in the task.

Increased dimension change-related activation was observed in the left frontopolar cortex, in the same area we repeatedly found to be active following stimulus-driven dimension changes (Pollmann et al., 2000; Weidner et al., 2002). The absence of response

change-related activation in the left FPC is consistent with the absence of frontopolar activation in previous task-switching experiments, which required stimulus-response re-mappings (Brass & von Cramon, 2002; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Rushworth, Hadland, Paus, & Sipila, 2002). Similarly, there is no reason to believe that left frontopolar activation reflects the inhibition of a prepotent response. Dimension changes occurred as frequently as dimension repetition trials, furthermore, target present trials occurred as often to color-defined as to motion-defined targets. Thus, there was no reason for a prepotent response to be established. Furthermore, functional imaging studies of the Stroop task have not reported frontopolar, but rather dorsolateral prefrontal and anterior cingulate activation in relation to inhibition of the prepotent response (Barch et al., 2001; Milham, Banich, & Barad, 2003; Peterson et al., 2002). Thus, the left FPC is involved in changes of perceptual, rather than response-related, origin; that is, presumably, in the reallocation of attentional resources from the old to the new target-defining dimension (Found & Müller, 1996).

Change-Related Functions of Anterior Prefrontal Cortex

As mentioned in the introduction, the anterior prefrontal cortex was not typically related to shifts of attention in past imaging studies. Shifts of visuospatial attention have not usually led to frontopolar activation (e.g., Corbetta et al., 1998; Gitelman et al., 1999; Pollmann & Morillo, 2003; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001; Yantis et al., 2002).

One characteristic of cross-dimensional singleton search that sets it apart from most previous studies of attention shifts is dimensional uncertainty. Endogenous cueing studies generally use cues of high validity. Exogenous cues capture attention automatically. If anterior prefrontal activation was observed in these paradigms, it was related to invalid exogenous cues (Lepsien & Pollmann, 2002). Likewise, task switching and dual task experiments are characterized by a clear rule-guided association between stimulus and response. In the task switching paradigm, the association between a given stimulus characteristic and the required response may change, but again, this change follows a deterministic rule.

The situation is different in singleton search. Here, subjects have to respond to an odd-one out stimulus, but they do not know how the singleton will differ from the distractors. As numerous studies have shown, the uncertainty about which visual di-

mension will contain the singleton target-defining feature leads to reaction time costs.

Anterior prefrontal activation has also been observed in other paradigms that share a component of uncertainty. This is the case with ambiguous target defining dimensions in the Wisconsin Card Sorting Test (WCST; Nagahama et al., 2001, Rogers, Andrews, Grasby, Brooks, & Robbins, 2000) and ambiguous word primes in cued recall (Henson, Shallice, Josephs, & Dolan., 2002). Attentional changes related to the stimulus dimension in the WCST involving the anterior prefrontal cortex, could be differentiated from switches of stimulus-response associations, which activated posterior prefrontal cortex (Nagahama et al., 2001). Taken together, this evidence suggests that the 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 in patients with anterior frontal lesions (Burgess, Veitch, de Lacy Costello, & Shallice, 2000; Goel, Grafman, Tajik, Gana, & Danto, 1997) and prospective memory (Burgess, Quayle, & Frith, 2001).

In contrast, task switching studies have so far not led to frontopolar activation (Brass & von Cramon, 2002; Dove et al., 2000; Rushworth et al., 2002). These paradigms have in common that the changes between tasks are governed by explicit rules. However, a dual task study found an activation at the border of the Brodmann areas 10 and 46 in the left hemisphere, i.e., at the posterior border of the anterior prefrontal cortex (Szameitat, Schubert, Müller, & von Cramon, 2002). This activation was especially pronounced when the temporal order of tasks was randomly varied across trials.

Although null effects always have to be interpreted with caution, these studies may demonstrate that executive processes involved in change-behavior per se do not drive frontopolar activation. They also show that the ambiguity about the appropriateness of an attention change is not a general feature of tasks with high executive demands. In fact, most tests of executive functions lack this ambiguity, which may have led to the absence of frontopolar activation in most studies of working memory and executive functions, as mentioned in the Introduction.

One study found left frontopolar activation to correlate with increasing task complexity in the Tower of London task, which is used to tap planning processes (van den Heuvel et al., 2003). However, task complexity itself can certainly not explain why we observed change-related frontopolar activation in easy pop-out search tasks, but not in the much more demanding singleton conjunction search task (Pollmann et al., 2000, Weidner et al., 2002). Likewise,

attention-change-related frontopolar activation was observed in an exogenous, but not an endogenous spatial cueing task (Lepsien & Pollmann, 2002, Pollmann & Morrillo, 2003). Moreover, singleton feature search is certainly less demanding than the bulk of tests of executive functions that do not lead to frontopolar activation, e.g., the Stroop task.

Specific Change-Related Functions

However, what is the specific contribution of the anterior prefrontal cortex in such situations of uncertainty? We have previously argued that phasic dimension-change-related activation in the left frontopolar cortex speaks against a sustained state of divided attention supported by this area (Pollmann et al., 2000). When we take into account that the frontopolar cortex was selectively involved in visual dimension changes, but not in response changes (Pollmann et al., 2004), we can conclude that this area is involved in some way in the attentional weighting of visual dimensions in singleton search. However, this involvement can take different forms. It may be that the left frontopolar cortex is directly involved in the allocation of attention to visual dimensions, i.e., as a unit that controls the neuronal modulation in occipital input units (Pollmann et al., 2000). However, the frontopolar cortex may have a function as a change detector as well, in that it detects relevant environmental changes, which are communicated to posterior brain areas, e.g., in the SEF, the FEF, or the parietal cortex, which themselves may direct the allocation of attention to visual dimension-specific modules in the occipital cortex.

I will first review evidence for a direct involvement in attentional change, and secondly review evidence in favor of the alternative, a role of the frontopolar cortex in change detection.

Direct Involvement in Attention Change

A direct involvement in the reallocation of attention can take two forms, facilitation of the new dimension or inhibition of the old. Owen et al. (1993) observed that patients with frontal lobe damage were worse in shifting attention from a previously relevant dimension of the Wisconsin Card Sorting Test (WCST; Grant & Berg, 1948) to an entirely new dimension (perseveration), whereas they were not impaired in shifting attention to a previously irrelevant dimension (learned irrelevance). In the WCST, stimulus cards have to be matched either by color, shape, or number of items on a card. Initially, the subject has to guess the correct dimension. When the correct di-

mension has been learned via feedback, the experimenter changes the relevant dimension and subjects have to adjust their card selection accordingly. Owen et al. interpreted their data as a deficit in inhibiting (or disengaging from; in the terminology of Posner, Walker, Friedrich, & Rafal, 1984) the old dimension, rather than an inability to switch to a new dimension. The variability in their patients' lesions, however, did not allow conclusions to be drawn regarding the part of prefrontal cortex which, when lesioned, may lead to this deficit.

A recent event-related fMRI study may shed some light on this issue (Konishi, Jimura, Asari, & Miyashita, 2003). Konishi et al. used a variant of the WCST in which their subjects were cued in certain intervals to shift to a specified new dimension. However, for a number of trials following the cue, the old dimension would remain valid. Thus, when subjects selected the target by its color, and were now cued to select by form, both selection by form and color would be correct for a number of trials, until the selection by color would become invalid. The idea behind this procedure was to dissociate processes involved in changing to the new dimension from processes involved in inhibition of the old dimension. Konishi et al. observed a left anterior prefrontal activation (in anterior middle frontal gyrus, bordering superior frontal sulcus) at the time when the old dimension became invalid, suggesting that this area was involved in the inhibition of (or disengagement from) the old dimension.

Change Without Awareness?

Interestingly, Konishi et al. (2003) found that the left anterior middle frontal gyrus was only active when subjects were not informed about the manipulation of the old dimension's validity and did not report any knowledge of it after the experiment, suggesting that left anterior prefrontal cortex supports unconscious inhibition of the old dimension. When the subjects of Konishi et al. were informed about the validity manipulation of the old dimension, a different pattern of activation was observed. The anterior middle frontal gyrus activation was not observed anymore, instead more posterior and inferior prefrontal activations, commonly observed in tasks which require explicit rule changes (e.g., task switching; Dove et al. 2000, Brass & von Cramon 2002) were observed. This is paralleled by our finding of dimension change related to left frontopolar activation in singleton feature search, in which subjects' dimension changes are stimulus triggered (and may sometimes not even reach awareness), and its absence in singleton conjunction search, which requires endoge-

nously controlled dimension changes (Weidner et al., 2002).

The activation observed by Konishi et al. (2003) was posterior to our frontopolar activation and may represent a different function. Nevertheless, it is remarkable that both Konishi et al. and our data suggest a role of the left anterior prefrontal cortex in cognitive changes that occur in the absence of conscious control mechanisms (see Pollmann 2001). Another parallel is the involvement in inhibitory processes. While we cannot discriminate between facilitatory and inhibitory functions in our dimension weighting experiments, left frontopolar involvement in the inhibition of attentional capture by salient stimuli was suggested by an event-related fMRI study of reflexive visuospatial attention (Lepsien & Pollmann, 2002). In this study, we found left frontopolar activation, at the same location as in the dimension-weighting experiments, in trials in which invalid cues were followed by contralateral target presentation at short latency, accompanied by response time costs. Attentional capture by peripheral cues itself did not lead to frontopolar activation. In analogy, left frontopolar cortex may be involved in visual dimension weighting by inhibition of the old dimension, rather than facilitation of the new dimension.

In summary, left anterior prefrontal cortex may have a specific role in the control of attention in that it contributes to the inhibition of a previously relevant stimulus dimension, in this way facilitating the change to a new dimension. However, this control function is specifically observed in situations in which there is no explicit rule which indicates when to change and, conversely, anterior prefrontal contribution seems to be not necessary when there is such a rule. This leads us to another aspect of anterior prefrontal cortex function.

Episodic Change Detection as a Potential Frontopolar Function

The anterior prefrontal cortex may have a role in the detection of task-relevant changes in the environment. Such a function would be compatible with the observation that frontopolar activation is often observed in tasks with some stimulus uncertainty. Change detection, as used in this context, does not mean detection of specific, predetermined targets, but rather an evaluation whether a change in the environment requires a shift of attention. Detection of task-relevant changes (leading to the inhibition of the old dimension) requires the comparison of stimulus attributes (such as the color and movement direction of the singleton) in the current trial and the previous trials. The 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. Furthermore, activation strength in the frontopolar cortex correlates with the amount of proactive interference (Henson et al., 2003). Specifically, frontopolar activation was high when a stimulus word from a word pair was in previous trials paired with different words than in the present trial. This pattern resembles the situation in singleton search or in the WCST, where the target-defining dimension changes over trials. A comparison between previous and current stimulus characteristics may be especially important in tasks which allow automatic processing in order to keep the flexibility to respond adequately to changes in the environment. Such a comparison depends on what has been called "source memory", i.e., the memory under what circumstances a particular item was encoded. Recently, the left frontopolar cortex, though more lateral and inferior than the activations reviewed above, was reported to support source memory selectively (Dobbins, Foley, Schacter, & Wagner, 2002). More posterior left inferior frontal areas, in contrast, showed activations related to both source and item memory. The task asked for explicit recollection of the circumstances of encoding, in contrast to the tasks of interest in this paper, which may be one potential reason for the different location of activation in the frontopolar cortex. Nevertheless, the distinction between anterior inferior frontal activation (reaching into the frontopolar cortex) associated with source memory, and more posterior inferior frontal activation related to both source and item memory may support the idea that the left anterior prefrontal cortex may have a specific role in episodic memory, which may be utilized for the control of attention whenever the subject is forced to search for an ambiguously defined target and has to shift attention between visual dimensions.

Relation to Other Concepts of Frontopolar Function

Christoff and colleagues (Christoff & Gabrieli, 2000; Christoph et al, 2001; Christoph, Ream, Geddes, & Gabrieli 2003) proposed that the anterior prefrontal cortex houses the top of a hierarchy of cognitive processing, in the sense that it supports abstract relational processing, as needed in difficult problems of the Raven's matrices, for instance, or, more generally, that it supports processing of internally generated information. It is difficult to see how this concept may apply to our very simple singleton search task. Nevertheless, there are commonalities in that frontopolar

activation was observed in tasks that required switches between (internally represented or external) dimensions. Our data suggest that not the complexity of internal thought processes is decisive for frontopolar involvement, but that it may rather be specific processes such as episodic monitoring and inhibition, as outlined above, which require the left frontopolar cortex.

Another account of frontopolar function was proposed by Koechlin and colleagues, who postulated that the frontopolar cortex might be involved in carrying out a secondary task while holding a primary task in working memory; a process they termed cognitive “branching” (Koechlin et al., 1999). Branching does not seem to be involved in our tasks. In cross-dimensional singleton search, there is no need for holding the old dimension in working memory while switching to the new dimension. If at all, such a process might be useful in search for conjunction targets, in the sense that one keeps the already searched items in working memory when switching to a new secondary dimension, in order not to return to already searched items. However, we observed frontopolar activation in single feature search, where this strategy is not needed, and not in conjunction search.

Thus, our data do not support the concept that cognitive branching to an episodic subtask, while the primary task is kept in working memory, is necessary to obtain frontopolar activation. However, our view that the left frontopolar cortex is involved in episodic monitoring and facilitates shifts of attention (by inhibition of the old dimension) when the target dimension changes, fits very well into the hierarchical model of prefrontal function recently proposed by Koechlin et al. (2003). They presented evidence for a hierarchy of processing steps from simple stimulus-response associations processed in the premotor cortex (BA 6), to context-dependent processing in the posterior prefrontal cortex (BA44/45), and on to episodic processing in more anterior parts of the prefrontal cortex (BA 46), still posterior to, but bordering the anterior BA 10 discussed in this paper.

In this context, the frontopolar cortex may elicit attentional control in situations in which episodic monitoring reveals changes in the task-relevant stimuli, which afford a reallocation of attention for optimal processing, even when this change is not governed by explicit instructions. The reallocation of attention may be facilitated by the inhibition of the old stimulus dimension (or the attended object or location). Further research will have to show whether the frontopolar cortex is involved both in change detection and inhibition, or preferentially in one of these processes.

Conclusion

In conclusion, the anterior prefrontal cortex may be at the top of a cascade of processes which control the allocation of attention. Anterior prefrontal activation was found when adaptive shifts of attention occurred without being governed by an explicit rule or exogenous cue. The anterior prefrontal cortex may subservise the detection of environmental changes that ask for a reallocation of attentional resources, specifically the inhibition of the previously attended dimension, location, or object. The involvement of this cortex is not dependent on high attentional or executive demands, instead, it was observed in tasks that allow rather automatic processing or in the absence of conscious awareness. These concepts are still speculative and require further empirical testing. Further studies will most likely find a differentiation between distinct areas in the anterior prefrontal cortex and their associated functions. However, the concepts developed above provide testable hypotheses that may lead us to a deeper understanding of the processes subserved by an, as yet, functionally not well charted part of the brain. Conversely, the integration of functional neuroimaging data on anterior prefrontal function may also lead to new testable hypotheses about the cognitive processes involved in the control of attention.

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