

Research report

Prefrontal regions play a predominant role in imposing an attentional ‘set’: evidence from fMRI

Marie T. Banich*, Michael P. Milham, Ruth Ann Atchley, Neal J. Cohen, Andrew Webb, Tracey Wszalek, Arthur F. Kramer, Zhi-Pei Liang, Vikram Barad, Dan Gullett, Chirag Shah, Colin Brown

The Beckman Institute, University of Illinois, Urbana-Champaign, 405 N. Mathews, Urbana, IL 61801, USA

Accepted 23 February 2000

Abstract

fMRI was used to determine whether prefrontal regions play a predominant role in imposing an attentional ‘set’ that drives selection of task-relevant information. While monitoring for an atypical item, individuals viewed Stroop stimuli that were either colored words or colored objects. Attentional demands were varied, being greater when the stimuli contained two distinct and incongruent sources of information about the task-relevant attribute (e.g., when attending to color, seeing the word ‘blue’ in red ink) as compared to only one source (e.g., seeing the word ‘late’ in red ink). Prefrontal but not anterior cingulate regions exhibited greater activation on incongruent than neutral trials, suggesting that prefrontal cortex has a major role in imposing an attentional ‘set’. In addition, we found that prefrontal activation is most likely to occur when that attentional set is difficult to impose. © 2000 Elsevier Science B.V. All rights reserved.

Theme: Neural bases of behavior

Topic: Cognition

Keywords: Attention; fMRI; Dorsolateral prefrontal cortex; Anterior cingulate; Stroop task

1. Introduction

Traditionally, frontal regions of the brain have been considered to be responsible for ‘executive control’ (see [1], Chapter 10, for a review). Although there is no agreement or precise definition of executive control, it has been used to subsume a wide variety of functions including the ability to create a plan or goal, to monitor progress towards that goal, to oversee the organization of action, and to override stereotypical responses. It has been suggested that frontal regions play such an executive function for a wide variety of cognitive abilities including memory [42] and attention [6,29]. In this paper, our goal is to discern the area(s) of frontal cortex associated with a specific executive aspect of attentional control, namely the ability to create an attentional set that allows the brain to

hone in on sources of information that are task-relevant [17].

Our prior neuroimaging work provides evidence that frontal regions, including dorsolateral prefrontal and cingulate cortex, are important for executive aspects of attention that aid in the selection of task-relevant information [2]. In these studies we used variants of the Stroop task. This task is commonly employed in studies of attentional selection [18,19], and has been found to be sensitive to damage in prefrontal regions [26,15,41]. In the standard color-word Stroop task, individuals must attend to and identify the ink color in which a word is written, while inhibiting the more automatic response of reading the word. The need for attentional selection is high in the incongruent condition in which the word’s identity (i.e., the semantic information and its associated responses) conflicts with the color in which it is written (e.g., the word ‘BLUE’ written in green). Less attentional selection is required in the neutral condition in which the word’s identity is unrelated to color (e.g., the word ‘DOOR’ written in green).

*Corresponding author. Tel.: +1-217-244-1264; fax: +1-217-244-8371.

E-mail address: mbanich@s.psych.uiuc.edu (M.T. Banich).

We found that patterns (topography) of activity within frontal regions produced by an increased need for attentional selection are *dependent* on the nature of information that is task relevant (i.e., color, spatial), suggesting a special organization of this brain region for selecting task-relevant information. Second, we demonstrated that patterns of activity within frontal regions are *relatively independent* of the type of information that is task-irrelevant. Hence, frontal areas appear to have a special sensitivity to task-relevant information, making them a leading candidate for the function of imposing an attentional set.

Our evidence for these assertions came from two experiments in our laboratory. In the first experiment, we employed two Stroop tasks that differed in the nature of the task-relevant dimension, but shared the same type of task-irrelevant dimension (i.e., a word's identity that needed to be ignored). By holding the task-irrelevant dimension constant across the two tasks, we could determine whether attentional effects within a given brain region are dependent upon the nature of the task-relevant dimension. In the second experiment we took the converse approach: we varied the nature of the task-irrelevant dimension across two tasks, but kept the task-relevant dimension constant (i.e., required a decision based on color). In this case, we were able to determine which brain regions are modulated during attentional selection by the task-irrelevant information.

These experiments yielded three important results. First, we verified a role for frontal regions in attentional control, as activation in these areas was greater in both experiments when there was a greater need for attentional selection (i.e., during incongruent as compared to neutral trials). Second, we observed that depending on the task-relevant attribute, different subregions within both dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC) became activated with an increased need for attentional selection. Activation was centered in more ventral regions when individuals had to attend to color, whereas it was centered in more dorsal regions when they had to attend to the spatial relationship between items. Third, we found that when individuals had to attend to color, similar regions of the DLPFC and ACC became activated regardless of whether the task involved ignoring the identity of a word or an object. These findings confirm that the subregion of DLPFC and ACC that becomes active during attentional selection is dependent on the nature of task-relevant information but relatively independent of the nature of task-irrelevant information.

Because similar patterns were found for both the DLPFC and the ACC we wished to investigate whether the ACC acts in concert with DLPFC to impose an attentional set, or whether each of these frontal regions is involved in different aspects of attentional selection. At present, the data available in the literature do not allow one to disambiguate between these two possibilities, as there is

evidence for both viewpoints. Studies of both animals and humans provide evidence suggesting that prefrontal regions play a role in imposing an attentional set. In monkeys, the activity of at least a subset of neurons in lateral prefrontal cortex appears to prospectively code for the expectancy of an anticipated choice in a delayed paired associate task [32]. In humans, switching between two or more different tasks in which individuals must systematically change their expectancy about task demands [33] appears to rely on dorsolateral prefrontal cortex (DLPFC) and associated areas. Neuroimaging data from PET [20] reveal that the left DLPFC is more active when participants are required to alternate between shape and color discriminations as compared to making just one of these decisions.

Although suggestive, none of the above data definitively supports the idea that prefrontal regions play a principle role in creating or maintaining an attentional set. Whereas prospective processing of information about objects occurs for cells in prefrontal cortex, this phenomenon has also been observed in other brain regions, such as inferior temporal cortex [34]. With regards to task switching in humans, it is not clear if these frontal areas are responsible for setting and maintaining biases about task requirements or whether they are specifically linked to the ability to *switch* between different task expectancies.

There is also evidence that the cingulate may play an important role in imposing an attentional set. Early neuroimaging studies of the Stroop task were more consistent in yielding activation of the ACC as compared to the prefrontal cortex [24,3,13,4]. These results have contributed to some researchers characterizing the ACC as playing a pre-eminent role in executive aspects of attention [29]. Furthermore, in numerous neuroimaging studies of executive function, co-activation of the ACC and DLPFC is observed [8,10,13,20,27,30].

Yet there are a variety of sources of data that suggest that the cingulate's role in attentional selection may be quite distinct from that involved in imposing an attentional set. First, there is evidence suggesting that activity of the ACC does not always accompany processing of incongruent Stroop stimuli. Taylor et al. [38] found prefrontal but not cingulate activity when taboo words or false fonts rather than neutral words were used as a baseline against which to compare activation for incongruent color words. Second, there are numerous alternative theories about the role of the ACC in attention ranging from response selection [25], to anticipation [23], to detecting and compensating for error [21], to the detection of conflict [5]. These findings raise the possibility that ACC activity in our prior studies was generated for reasons other than creating and maintaining an attentional set.

To disentangle the role that the DLPFC plays in imposing an attentional set as compared to the ACC, we considered the design of our prior studies. We realized that incongruent as compared to neutral trials engender a high

degree of response competition [25] and potential for error [5], two factors previously linked to cingulate activity. Hence, we decided to change our task such that these factors (response competition, potential for error) were held as constant as possible across conditions differing with respect to the need for attentional selection (i.e., incongruent vs. neutral trials).

To minimize the effects of response competition and potential for error, we modified the instructions provided to subjects, but retained use of the same stimuli and comparison (incongruent vs. neutral) as in our previous work. Rather than identifying in which of three colors an item appeared, we had participants monitor for the appearance of an atypical item, such as a purple stimulus, when items were presented in a limited set of colors, such as red, green, and orange. Participants were told that such an atypical item might or might not occur once during the course of each run, and that they would have to indicate whether or not such an item did appear. Under such task instructions, the likelihood of an error or response conflict is much more equivalent for incongruent and neutral items. For example, the word 'RED' displayed in yellow is no more likely to be considered purple than will the word 'LOT' displayed in yellow.

Despite these task modifications, the region that is mainly responsible for imposing an attentional set should still yield greater activity on incongruent than neutral trials. On incongruent trials, both the task-relevant dimension and the task-irrelevant dimension contain information related to the attentional set (e.g., both the word 'red' and its ink color blue are related to the attentional set for color). Proper task performance requires a separation of these two sources of color information to determine which one is task-relevant. In contrast, on neutral trials, only the task-relevant dimension, the item's ink color, contains information related to the attentional set (i.e., the word 'lot' has no relevance with regards to color), and no disambiguation between the sources of color information is required. Hence, any area that is mainly involved in imposing an attentional set should be more engaged on incongruent than on neutral trials. We predict that the DLPFC will exhibit such a pattern.

In contrast, any brain region that is related to response conflict or error detection rather than the imposition of an attentional set, should yield little or no difference in activation on incongruent versus neutral trials. One of the strengths of the current experiment is that we have obtained increased activity in both ACC and DLPFC on incongruent as compared to neutral stimuli in our prior study which used the same stimulus set and attentional contrast as well as a similar statistical approach [2]. Hence, a lack of increased activation on incongruent versus neutral trials in the current study for either the ACC or DLPFC would be quite telling. We predict that the ACC will not show a difference in activity on incongruent as compared to neutral trials, which would implicate a role in response

conflict and/or error detection, rather than a role in imposing an attentional set.

A second objective of the current study was to determine whether prefrontal activation is linked to the difficulty of imposing an attentional set. Many theories of frontal lobe function emphasize that this brain region is involved when a non-routine (i.e., novel) situation is encountered and guided control over behavior is imperative. For example, the theory of Stuss and Benson [36] suggests that the frontal lobes are highly operative when behavior must be tightly regulated via conscious control, when information must be organized to reach a goal, or when the situation is atypical. Similarly, Shallice [35] assumes that the frontal lobes are important for controlling behavior via the supervisory attentional system. This system is invoked when there is no pre-existing linkage between a stimulus and behavior, when a task is difficult, when problem solving is required, and when the typical tendency to respond must be overcome or inhibited. In both of these models, the frontal lobes become more critical as tasks become less routine and controlled attention must be exerted to ensure correct performance.

Coupling this work with our prior neuroimaging results [2], we wished to investigate whether prefrontal involvement would vary with the degree to which attentional control must be exerted to process task-relevant information. In particular, we predicted that increased prefrontal activation on incongruent as compared to neutral trials would be most likely to be observed when processing of the task-relevant dimension requires more attentional control than processing of the task-irrelevant information as compared to vice versa. If processing of the task-irrelevant information occurs with little attentional control (e.g., a word is read relatively automatically), then it will be more readily available to influence performance than will the task-relevant information (e.g., the word's ink color). On incongruent trials, the task-irrelevant dimension contains information relevant to the attentional set. In such a situation, prefrontal mechanisms will need to select and prioritize the task-relevant information over the task-irrelevant information (e.g., a set must be imposed to monitor for a word depicted in purple, not the word 'purple'). In contrast, if the more automatically processed dimension is task-relevant, then it will not be as difficult to impose the correct attentional set.

We used color-word and color-object Stroop stimuli to explore this hypothesis. Like the color-word Stroop stimuli, color-object stimuli consist of colored items. For an incongruent color-object stimulus, an object is depicted in a color different than the one with which it is strongly associated (e.g., a blue strawberry when strawberries are strongly associated with the color red). Neutral trials are those in which the object is depicted in one of many colors with which it is associated (e.g., a blue car).

With these color-word and color-object stimuli, we were able to contrast conditions in which the processing of color

is either more attentionally demanding or less attentionally demanding than that of the other dimension. When viewing color-word Stroop stimuli, processing of color is *more* demanding (i.e., less automatic) than that of the word [7]. In contrast, for color-object Stroop stimuli, color is a fundamental feature of visual processing [40] and hence it is *less* demanding to direct attention to this feature as compared to directing attention to an object, which involves higher-order visual processing areas [39].

If prefrontal activation is linked to the difficulty of imposing an attentional set, then different patterns of prefrontal activation should be observed when attending to color with the color-word stimuli as compared to the color-object stimuli. To investigate this issue, we varied, for each type of stimulus, whether the individual was instructed to attend to color or was instructed to attend to the item (i.e., the word or the object). For the color-word Stroop stimuli, we expected that increased attentional demands would result in more prefrontal activity when attending to color than to the word because with these stimuli it is more attentionally demanding to attend to the color than the word. In contrast, for the color-object Stroop stimuli, we predicted that increased attentional demands would produce more prefrontal activity when attending to the object than the color because in this task object processing is more attentionally demanding than color processing. Notice that such a contrast provides an extremely strong test of our hypothesis because for both types of stimuli we have a condition in which an individual is attending to color. If our hypothesis is wrong and the results are driven solely by the nature of the task-relevant dimension (e.g., color vs. identity), then we should obtain similar patterns for both types of stimuli when attention is directed to color. Also notice that such an approach provides another method for differentiating the role of the prefrontal and cingulate regions. If prefrontal regions play a predominant role in imposing an attentional set, then prefrontal activity should co-vary with how demanding it is to direct attention to the task-relevant dimension, but that of the cingulate should not.

In summary, the objectives of our study were twofold. First, we wished to investigate the hypothesis that prefrontal areas play a prominent role in creating and maintaining an attentional set. Second, we wished to test the hypothesis that the degree to which prefrontal areas are involved in imposing such a set depends on how attentionally demanding it is to direct attention to the task-relevant dimension.

2. Materials and methods

2.1. Subjects

Twelve right-handed, native English-speakers served as volunteers, but data for two were lost due to technical difficulties, leaving a sample of 10. All were screened to

ensure that they did not have a history of neurological insult.

2.2. Stimuli

2.2.1. Color-word stimuli

Two sets of three ink colors were employed for the presentation of words, one for each color-word task (attend to form, attend to color): (1) blue, brown, and yellow, and (2) red, orange, and green. For each color-word task, there were two sets of stimuli: incongruent words in which the word names an ink color other than that in which it is printed (e.g., the word 'BLUE' printed in yellow) and neutral words that are unrelated to color (e.g., notion, chain, lost). Neutral words were matched with the color words for word frequency and length [16]. The assignment of color and word sets to the two tasks was counterbalanced across subjects.

2.2.2. Color-object stimuli

Two sets of colors were used for the presentation of objects, one for each color-object task (attend to form, attend to color): (1) red, orange, and green, and (2) yellow, orange, and green. For each color-object task, there were two sets of objects: a set of objects strongly associated with a color in the task's color set (high-association objects) (e.g., strawberry, pumpkin, lizard in one set and sun, carrot, frog in the other), and a set of objects that are not strongly associated with any color (low-association objects) (e.g., car, yarn, flag, book, flower). The assignment of color and object sets to the two tasks was counterbalanced across subjects.

We determined the strength of association between colors and objects in a norming study. 20 participants were asked to name the colors that first came to mind for each object. Across subjects, the mean number of colors reported for incongruent stimuli was 1 (std. dev.=0), while for the neutral stimuli the mean number of colors reported was 4 (std. dev.=1.03). Then we asked participants to rate on a 7-point scale the frequency with which they would expect the first color that they mentioned to be associated with that object (1=only some of the time, 7=all of the time). For incongruent stimuli the mean rating was 6.52 (std. dev.=0.25), while for the neutral stimuli, the mean rating was 2.23 (std. dev.=0.60).

Incongruent trials were constructed by presenting a high-association object in each of the two possible colors from the task color set that is different from the one with which it is typically associated (e.g., a red carrot). For neutral trials, we used low-association objects depicted in one of two colors from the task color set (e.g., a red flag). In this manner, each neutral and incongruent item could appear in one of two possible colors.

2.3. Design

Within each of 4 runs, blocks of neutral trials (off blocks) were alternated in a 4.5 cycle boxcar design, with blocks containing 50% neutral and 50% incongruent trials (on blocks). There were 18 trials per block. In one set of two runs, they viewed a series of objects, and in the other set of two runs they viewed a series of words. In one run within each set, individuals were instructed to attend to the color of the item, and in the other to the nature of the item. More specifically, when individuals had to attend to color, individuals had to monitor a series of items (either words or objects) and determine whether any of the items was ever presented in a particular color (i.e., purple). They were informed that such occurrences were quite rare, but that they were to monitor carefully for such an item nonetheless. In fact, none of the items ever appeared in purple. At the end of the run, the individual was queried as to whether they had observed a purple item. Likewise, when told to attend to the item, participants were told to monitor whether an impossible item (a non-word in the case of the word task and a nonsense object in the case of the object task) ever appeared. As when attending to color, participants were informed that such occurrences were quite rare, but to carefully monitor for the item nonetheless. In fact, an impossible item never appeared. Nonetheless, at the end of the run, the individual was queried as to whether they had observed an impossible item. No participants ever reported seeing an atypical item. Table 1 summarized the design of the study. Order of the runs was counterbalanced across subjects.

2.4. Procedure

Participants were placed in a 1.5 Tesla GE Signa scanner and their position was stabilized by placing their mouth on a bite-bar attached to the head coil to minimize motion during the session. Visual stimuli were presented using a goggle system by Resonance Technologies. Stimulus presentation was controlled by a Pentium-based Dell IBM-PC compatible computer using MEL software.

For each subject's run, a total of 144 gradient echo EPI data sets were acquired (TR=2400 ms, TE=40 ms, flip angle=90 degrees), consisting of 15 contiguous slices (thickness=7 mm, 3.75×3.75 mm). In addition, a 3D gradient echo anatomical set was acquired for each participant for the purpose of landmark selection.

2.5. Data analysis

The first six volumes of each run were discarded to allow the MR signal to reach steady state. Prior to statistical tests, images in the data were convolved with a 2D Gaussian kernel (FWHM=10.5 mm), temporally denoised using an ID-wavelet transform (visu-shrink, number of levels=4), and linearly detrended (parameter estimates based upon images in the off phases only). An unpaired *t*-test test was used to generate statistical probability maps between the on and off phases for each voxel for each run. A 4.8 second hemodynamic lag was assumed. The probability values from the unpaired *t*-test were then converted to *Z*-scores and averaging of *Z*-score maps across subjects was carried out in a common stereotaxic space [37]. MedX V2.1 was used to carry out image processing and statistical analyses. Activation maps were generated using a statistical threshold of average (*Z*)>1.96 (*P*<0.05), and single voxel activations were removed.

3. Results

3.1. Prefrontal regions

For the comparison between incongruent and congruent trials, we found increased prefrontal activation but only when participants attended to the more attentionally-demanding dimension in each task. For the color-word task, we only obtained activation when participants attended to color. This activation was located bilaterally in the inferior and middle frontal gyrus. To more precisely determine the location of this activation, we identified the peaks of activation [22]. Activation was centered in the inferior

Table 1
Overview of experimental design

Run	Task	Stimuli	Attention	Instructions	Trial types
1	Color-word	Colored Words	Attend Color	Monitor for a purple item	5 blocks: Neutral 4 blocks: 50% neutral/ 50% incongruent
2	Color-word	Colored Words	Attend Item	Monitor for a non-word	5 blocks: Neutral 4 blocks: 50% neutral/ 50% incongruent
3	Color-object	Colored Objects	Attend Color	Monitor for a purple item	5 blocks: Neutral 4 blocks: 50% neutral/ 50% incongruent
4	Color-object	Colored Objects	Attend Item	Monitor for a nonsense shape	5 blocks: Neutral 4 blocks: 50% neutral/ 50% incongruent

gyrus Brodmann Area (BA) 44 (Talairach coordinates: $x = -48$, $y = 10$, $z = 34$; $x = 50$, $y = 16$, $z = 34$) while activation within the middle frontal gyrus occurred within BA 46 ($x = -42$, $y = 28$, $z = 20$; $x = 54$, $y = 24$, $z = 26$). These regions within BA 44 and BA 46 overlap with that we have previously observed as attentional demands increase when color must be identified in the color-word Stroop task [2]. When participants attended to the word, we observed no prefrontal activity.

For the object task, we found activation in the right middle frontal gyrus (BA 9: $x = 40$, $y = 16$, $z = 30$) when participants attended to the object, but none when they attended to color (see Fig. 1). In our prior work [2], we found that increasing attentional demands also increased activity in a similar region of BA 9 when color had to be identified in the color-object task. This region of the right

hemisphere appears to become activated with increasing attentional demands when the task-relevant attribute is related to the ventral visual processing stream – objects in the present experiment and color in our prior experiment. Furthermore, this region is distinct from that activated in prior experiments by increased attentional demands when the task-relevant attributes relies on the dorsal visual-processing stream (e.g., categorical spatial information: above/below; left right). In that case, we observed activation in area 9 of the left hemisphere but not the right.

3.2. Cingulate regions

For both tasks, there was no increase in cingulate activity for incongruent as compared to neutral stimuli for either attentional set. The implications of this finding are

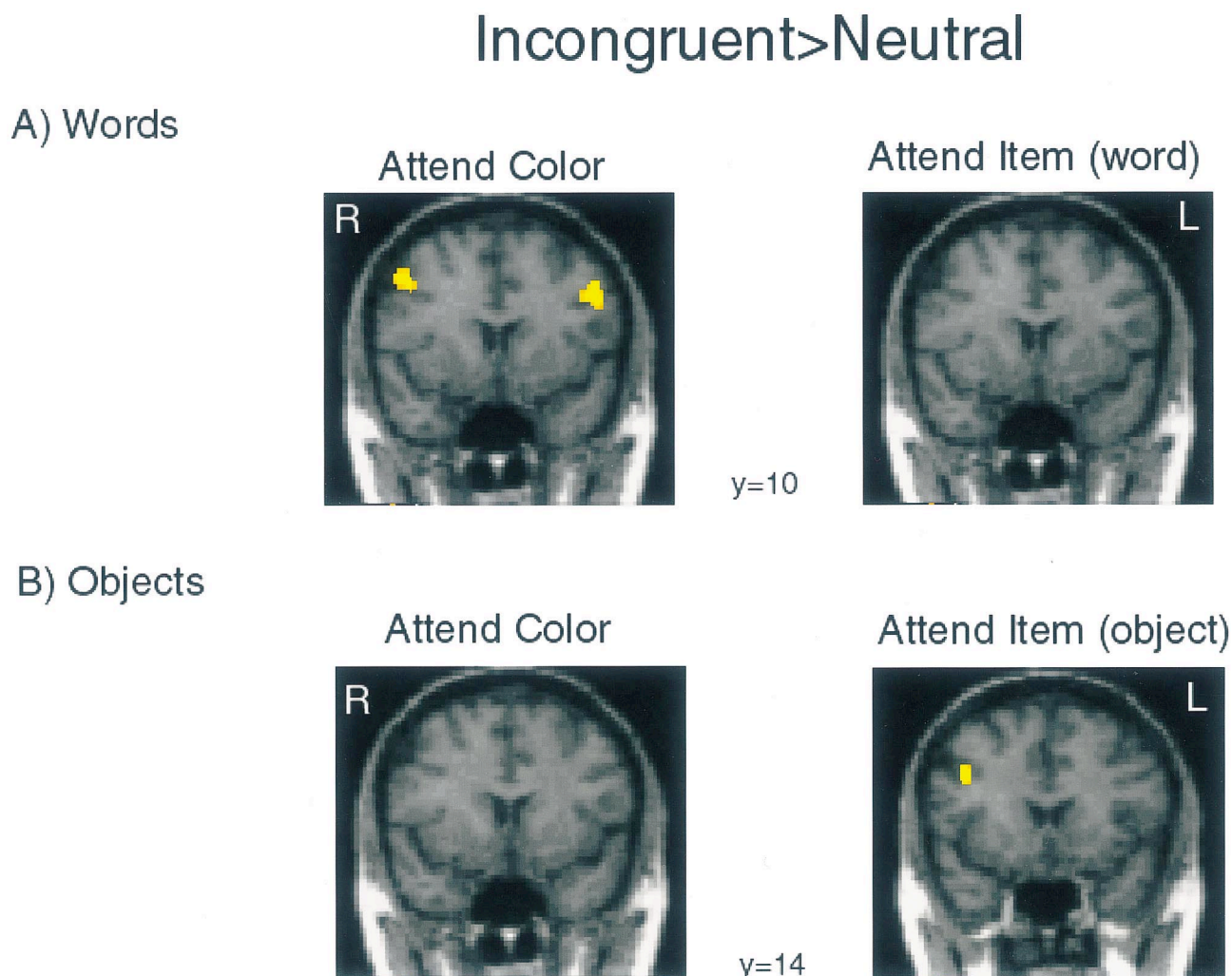


Fig. 1. Shown here are the prefrontal regions that were more highly activated for incongruent as compared to neutral stimuli. Radiological convention is employed so that the right side of the brain is depicted on the left side of space: (a) The pattern of results for the color-word stimuli. Notice that there was bilateral activity in prefrontal areas when it was more difficult to direct attention to the task-relevant dimension as compared to the task-irrelevant dimension (i.e., when attending to color). No such activity was observed when attending to the task-relevant dimension was less demanding than attending to the task-irrelevant dimension (i.e., when attending to the word); (b) The pattern of results for the color-object stimuli. Notice once again that there is prefrontal activity only when directing attention to the task-relevant dimension was more difficult than directing it to the task-irrelevant dimension. Here there is activity in the right middle frontal gyrus when attending to the item (i.e., the object) but not when attending to color.

clear when one considers that although our experimental design reduced differences between response conflict and selection on incongruent compared to neutral trials, it did not reduce the greater difficulty of imposing an attentional set on incongruent as compared to neutral trials. Hence, the lack of increased cingulate activity on incongruent trials suggests that it does not play a major role in imposing an attentional set. Rather, the results are consistent with suggestions that the anterior cingulate is involved in response selection [25] or error detection [5].

3.3. Extrastriate regions

In extrastriate regions, no increase in activity for incongruent as compared to neutral stimuli was noted for color-word stimuli. For the color-object stimuli, however, a bilateral increase in activity on incongruent as compared to neutral stimuli was noted at the juncture of the cuneus cortex and the lingual gyrus (BA 18: $x = 12$, $y = -84$, $z = 6$; $x = -16$, $y = -93$, $z = 8$) and in BA 19 in the left hemisphere ($x = -16$, $y = -92$, $z = 22$) when attention was directed to color. No difference in activation between incongruent and neutral trials was observed when attention was directed to the object.

4. Discussion

Our data strongly support the idea that the prefrontal region is primarily responsible for creating and maintaining an attentional set, especially when it is more difficult to direct attention to task-relevant information than to task-irrelevant information. For incongruent relative to neutral trials, we found increased activation of the DLPFC for both the color-word and color-object Stroop stimuli. Attentional demands were greater on incongruent trials because the task-irrelevant information was related to the attentional set (e.g., was related to color), yet had to be ignored. In such a case, it is imperative that the correct information channel be selected (e.g., selection of the channel with information about ink color as compared to the channel with word-related color meaning). We did not observe a similar pattern for the anterior cingulate suggesting that it does not play as prominent a role in imposing an attentional set as does DLPFC.

Other researchers have provided evidence that the DLPFC performs functions related to imposing an attentional set. Arguing on the basis of both neuroimaging, behavioral data and computational modelling, some researchers have suggested that prefrontal cortex is involved in providing the 'context' that helps to choose task-relevant information [6]. Others have suggested that the DLPFC is involved in the manipulation of the contents of working memory, as opposed to more ventral regions of prefrontal cortex that are involved in the maintenance of the contents of working memory [28]. Because activation

has been observed in the DLPFC of the right hemisphere regardless of the nature of information to be processed (e.g., spatial versus verbal), it has been suggested that this region is involved in control processes relevant to working memory (e.g., [42]). From this vantage point, one can conceptualize the DLPFC as playing a role in selective attention, choosing the relevant contents of working memory that are required to ensure correct task performance. Conversely, one can conceptualize the DLPFC's role in working memory as influencing attentional processing in that working memory may aid in keeping an online representation of the information that must be attended [31], which is critical for creating and maintaining an attentional set. Hence, like others [9], we consider there to be a close relationship between attention and working memory.

It is noteworthy that activation in prefrontal regions was only observed when it is harder to direct attention to the task-relevant dimension relative to the task-irrelevant dimension. Prefrontal activation increased when participants attended to the color but not the word in the color-word Stroop task, and when attending to the object but not color in the color-object Stroop task. This pattern suggests, therefore, that attentional control by the DLPFC mainly occurs when there is a need to override automatic or intrinsic attentional biases. Notice that the pattern of results precludes the possibility that the prefrontal activation is driven solely by the nature of the attended attribute. If that were the case, then prefrontal activity should have been identical for both types of Stroop stimuli when participants were required to monitor for an atypical color. The activity of the cingulate was not influenced by how difficult it is to direct attention to the task-relevant dimension over the task-irrelevant one, confirming that it does not play a prominent role in imposing an attentional set.

Our results also indicate a difference in activation in posterior regions between the color-word and color-object stimuli. More specifically, when attention was directed to color, there was activation of areas 18 and 19 for the color-object stimuli, but not for the color-word stimuli. We believe that this result can help inform us as to how learned associations may modify attentional processing. The relationship between form and color is not arbitrary for the objects we used, although it is for the words. We have a lifetime of seeing yellow bananas and red strawberries. Neither strawberries nor bananas come in blue, purple or black or any other color. Hence, for color-object stimuli, the object's form will activate a very specific color, the one in which it is typically seen. For example, processing an object, such as a banana, will activate a specific color, yellow. On incongruent items, the color typically associated with an object (e.g., yellow) is different than the one being viewed (e.g., red), a mismatch that according to our data can be detected in extrastriate regions. Indeed there is evidence that these extrastriate regions have been tuned by

experience to associate form and color. Zeki and Marini [43] found that the same left occipital region exhibits more activation to abnormally colored objects (e.g., a blue strawberry) than to a grey-scale version of those same objects. Because such activation does not occur when comparing multi-colored Mondrian stimuli to their grey-scale counterparts, it appears that these regions have stored specific information associating an item's typical color and form. Since damage to these same areas impairs visual priming [12], we speculate that such learning is implicit and occurs at the perceptual level. A similar effect is not observed for words because color words can appear in many different colors. The word 'blue' may appear in black, blue, red, yellow, green or any other color. In everyday reading, we are used to discarding and ignoring the color in which words are printed and directing attention just to the word's meaning.

We also believe that the nature of learned associations explains why no extrastriate activation was found when attention was directed to the object in the color-object task. Here the task-irrelevant dimension, color (e.g., yellow), is not going to strongly activate information about a specific object that could prominently interfere with the processing of an object being attended. Rather activation of a specific color (e.g., yellow) is likely to weakly activate a series of associations with a whole host of objects (e.g., daffodils, lemons, bananas, grapefruit, just to name a few). When attending to the color, in contrast, the presence of an object that has a typical color, even though task-irrelevant, will evoke an association to a very specific color that may interfere with the color being attended. This conflict appears to be detected in extrastriate cortex.

The results of the present study are consistent with our prior work [2] although they may not appear so at first glance. In the present study, prefrontal activity was no greater on incongruent than neutral trials for the color-object stimuli when the instruction was to attend to color. Yet in a prior experiment utilizing the same stimuli but requiring the color of the item to be identified via a 3-choice button press, this same contrast yielded prefrontal activity. Obviously, in both cases, incongruent trials (e.g., yellow strawberry) will provide conflicting information, as there will be a mismatch between the item's actual color and color with which that object is typically associated. The degree to which the prefrontal regions are required for attentional control, however, is likely to differ in the two studies because of variations in task demands. When a specific color must be identified, expectations about the canonical color of the items are more likely to cause interference than when an atypical color must be detected. For example, if we must identify a color as yellow, we have a strong expectation that strawberries are not yellow. In contrast, if one is just determining that an item is 'not purple', then there is likely to be less interference from a yellow strawberry, as both the item's actual color and its canonical color lead to the same conclusion that the item is

not purple. There will be a greater need for a prefrontal attentional set to override expectations that strawberries are red when the task requires the individual to identify the exact color of an item as compared to when the individual is just monitoring for an atypical color.

Finally, we would like to discount an alternative explanation for our results in the color-object task. One might consider the possibility that the right prefrontal activation in this task is being driven by the novelty of seeing an item in a non-canonical color. Prefrontal regions, especially those of the right hemisphere, have been noted to be involved in detecting novel items and situations [11,14], and activation is found in this region when viewing items in an atypical color [43]. Because of strong color-object associations, such neural mechanisms might be invoked when viewing our incongruent color-object stimuli because they are relatively novel (e.g., a red banana). We think that such an explanation can be discounted for two reasons. First, both the color-object and color-word stimuli produced similar degrees of right prefrontal activation. Yet, it is much more novel to see a red banana than to see a word such as 'blue' in an ink color other than black. Hence, if novelty were driving our results, we would have expected the right prefrontal activity to be greater for the color-object stimuli than the color-word stimuli, which was not the case. Second, increased activity in right prefrontal regions is not always observed for the incongruent (i.e., novel) color-object stimuli. Rather, we observe right prefrontal activity for the color-object stimuli only when attending to the object but not when attending to the color. Were activity driven merely by the novelty of seeing an item in an atypical color, we would have expected increased activation both when attending to the color and when attending to the object.

As a whole, our results provide important support for the idea that the prefrontal regions specifically act to provide an attentional set that allows for the selection of task-relevant information. In addition, our results provide evidence that the degree to which prefrontal regions must be invoked in this process increases as the attentional demands of imposing that attentional set increase.

Acknowledgements

This research was funded by the Beckman Institute for Advanced Science and Technology at the University of Illinois, Urbana-Champaign, and was performed with support from Carle Clinic.

References

- [1] M.T. Banich, *Neuropsychology: The Neural Bases of Mental Function*, Houghton-Mifflin, Boston, 1997.
- [2] M.T. Banich, M.P. Milham, R.A. Atchley, N.J. Cohen, A. Webb, T.

- Wszalek, A.F. Kramer, Z.-P. Liang, A. Wright, J. Shenker, R. Magin, V. Barad, D. Gullett, C. Shah, C. Brown, Distinct neural networks for the processing of attended and unattended information revealed by fMRI, *J. Cogn. Neurosci.*, in press.
- [3] C.J. Bench, C.D. Frith, P.M. Grasby, K.J. Friston, E. Pauesu, R.S.J. Frackowiak, R.J. Dolan, Investigations of the functional anatomy of attention using the Stroop test, *Neuropsychologia* 31 (1993) 907–922.
- [4] C. Carter, M. Mintun, J.D. Cohen, Interference and facilitation effects during selective attention: An H_2 ^{15}O PET study of Stroop task performance, *Neuroimage* 2 (1995) 264–272.
- [5] C. Carter, T. Braver, D. Barch, M. Botvinick, D. Noll, J.D. Cohen, Anterior cingulate cortex, error detection, and the online monitoring of performance, *Science* 280 (1998) 747–749.
- [6] J.D. Cohen, T.S. Braver, R.C. O'Reilly, A computational approach to prefrontal cortex, cognitive control and schizophrenia: Recent developments and current challenges, *Phil. Trans. R. Soc. Lond.* 351 (1996) 1515–1526.
- [7] J.D. Cohen, K. Dunbar, I.L. McClelland, On the control of automatic processes: A parallel distributed processing account of the Stroop effect, *Psychol. Rev.* 97 (1990) 332–361.
- [8] M. Corbetta, F.M. Miezin, S. Dornmeyer, G.L. Shulman, S.E. Petersen, Selective and divided attention during visual discrimination of color, shape and speed: Functional anatomy by positron emission tomography, *J. Neurosci.* 11 (1991) 2383–2402.
- [9] R. Desimone, J. Duncan, Neural mechanisms of selective visual attention, *Ann. Rev. Neurosci.* 18 (1995) 193–222.
- [10] C.D. Frith, K. Friston, P.F. Liddle, R.S. Frackowiak, Willed action and the prefrontal cortex in man: a study with PET, *Proc. R. Soc. Lond. B, Biol. Sci.* 244 (1991) 241–246.
- [11] J.M. Fuster, The prefrontal cortex, mediator of cross-temporal contingencies, *Human Neurobiol.* 4 (1985) 169–179.
- [12] J.D.E. Gabrieli, D.A. Fleischman, M.M. Keane, S.L. Reminger, F. Morrell, Double dissociation between memory systems underlying explicit and implicit memory in the human brain, *Psychol. Sci.* 6 (1995) 76–82.
- [13] M. George, T. Ketter, R. Parekh, H. Ring, B. Casey, M. Trimble, B. Horwitz, P. Herscovitch, R. Post, Regional brain activity when selecting a response despite interference: an H_2O PET Study of the Stroop and an Emotional Stroop, *Human Brain Mapping* 1 (1994) 195–209.
- [14] E. Goldberg, K. Podell, M. Lovell, Lateralization of frontal lobe functions and cognitive novelty, *J. Neuropsychiatry Clin. Neurosci.* 6 (4) (1994) 371–378.
- [15] C.J. Golden, Identification of brain disorders by the Stroop color and word test, *J. Clin. Psychol.* 32 (1976) 654–658.
- [16] H. Kucera, W. Francis, *Computational Analysis of Present-day American English*, Brown University Press, Providence, RI, 1967.
- [17] D.L. LaBerge, Attention, *Psychol. Sci.* 1 (1990) 156–161.
- [18] C.M. MacLeod, Half a century of research on the Stroop effect: An integrative review, *Psychol. Bull.* 109 (1991) 163–203.
- [19] C.M. MacLeod, The Stroop task: The 'gold standard' of attentional measures, *J. Exp. Psychology: General* 121 (1992) 12–14.
- [20] D.E. Meyer, J.E. Evans, E.J. Lauber, J. Rubinstein, L. Gmeindl, L. Junck, R.A. Koeppel, Activation of brain mechanisms for executive mental processes in cognitive task switching, Poster presented at the meeting of the Cognitive Neuroscience Society, 1997, Boston, MA.
- [21] W.H.R. Miltner, C.H. Braun, M.G.H. Coles, Event-related brain potentials following incorrect feedback in a time-estimation task: Evidence for a 'generic' neural system for error detection, *J. Cognit. Neurosci.* 9 (1997) 788–798.
- [22] M. Mintun, P. Fox, M. Raichle, Highly accurate method of localizing regions of neural activation in the human brain with positron emission tomography, *J. Cereb. Blood Flow and Metab.* 1 (1989) 96–103.
- [23] S. Murtha, H. Chertkow, M. Beauregard, R. Dixon, A. Evans, Anticipation causes increased blood flow to the anterior cerebral cortex, *Human Brain Mapping* 4 (1996) 103–112.
- [24] J.V. Pardo, P.J. Pardo, K.W. Janer, M.E. Raichle, The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm, *Proc. Natl. Acad. Sci. USA* 87 (1990) 256–259.
- [25] T. Paus, M. Petrides, C. Evans, E. Meyer, Role of the human anterior cingulate cortex in the control of oculomotor, manual, and speech responses: A PET study, *J. Physiol.* 70 (1993) 453–469.
- [26] E. Perret, The left frontal lobe of man and the suppression of habitual responses in verbal categorical behavior, *Neuropsychologia* 12 (1974) 323–330.
- [27] S.E. Petersen, H. van Mier, J.A. Fiez, M.E. Raichle, The effects of practice on the functional anatomy of task performance, *Proc. Natl. Acad. Sci. USA* 95 (1998) 853–860.
- [28] M. Petrides, Frontal lobes and behavior, *Curr. Opin. Neurobiol.* 4 (1994) 207–211.
- [29] M.I. Posner, S. DeHaene, Attentional networks, *Trends Neurosci.* 17 (1994) 75–79.
- [30] M. Posner, G. DiGirolamo, Executive attention: Conflict, target detection, and cognitive control, in: R. Parasuraman (Ed.), *The Attentive Brain*, The MIT Press, Cambridge, MA, 1998, pp. 401–423.
- [31] G. Rainer, W.F. Asaad, E.K. Miller, Selective representation of relevant information by neurons in the primate prefrontal cortex, *Nature* 393 (1998) 577–579.
- [32] G. Rainer, S.C. Rao, E.K. Miller, Prospective coding for objects in primate prefrontal cortex, *J. Neurosci.* 19 (1999) 5493–5505.
- [33] R.D. Rogers, S. Monsell, Costs of a predictable switch between simple cognitive tasks, *J. Exp. Psychology: General* 124 (1995) 207–231.
- [34] K. Sakal, Y. Miyashita, Neural organization for the long-term memory of paired associates, *Nature* 354 (1991) 152–155.
- [35] T. Shallice, Specific impairments of planning, *Philos. Trans. R. Soc. Lond. B* 298 (1982) 199–209.
- [36] D.T. Stuss, D.F. Benson, *The Frontal Lobes*, Raven Press, New York, 1986.
- [37] J. Talairach, P. Tournoux, *Co-planar Stereotaxic Atlas of the Human Brain*, 2nd Edition, Thieme, Stuttgart, 1988.
- [38] S.F. Taylor, S. Komblum, E.J. Lauber, S. Minoshima, R.A. Koeppel, Isolation of specific interference processing in the Stroop task: PET activation studies, *Neuroimage* 6 (1997) 81–92.
- [39] R. Tootell, A. Dale, M. Sereno, R. Malach, New images from human visual cortex, *Trends Neurosci.* 19 (1996) 481–489.
- [40] A. Treisman, G. Gelade, A feature integration theory of attention, *Cognit. Psychol.* 12 (1980) 97–136.
- [41] P. Vendrell, C. Junque, J. Pujol, M.A. Jurado, J. Molet, J. Grafman, The role of prefrontal regions in the Stroop task, *Neuropsychologia* 33 (1995) 341–352.
- [42] A.D. Wagner, Working memory contributions to human learning and remembering, *Neuron* 22 (1999) 19–22.
- [43] S. Zeki, L. Marini, Three cortical stages of colour processing in the human brain, *Brain* 121 (1998) 1669–1685.