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Lateral prefrontal damage affects processing selection but not attention switching

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Abstract

A challenge for cognitive neuroscience is to determine how the prefrontal cortex (PFC) contributes to the cognitive control operations that oversee thought and action. We studied the effects of damage to the lateral PFC in two types of attentional control. Subjects performed a choice reaction time task that required attention switching and processing selection. The performance of individuals with PFC or parietal cortex damage was compared with that of age-matched and young control subjects. Damage to the lateral PFC did not significantly impair the switch from attending to one color to attending to another. PFC damage did, however, significantly increase the effects of distractor stimuli, implicating the lateral PFC in processing selection. Individual subjects' performance suggested that the left inferior posterior PFC was the most critical for processing selection. Our data are consistent with the view that the lateral PFC contributes to the top-down control of the information flow along pathways from sensory input to motor output.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Prefrontal cortex; Attentional control; Conflict; Attention switching; Lesion

1. Introduction

In a complex, constantly changing environment, the human brain has the ability to select a limited subset of the available information for detailed processing, to ignore the rest, and to switch this focus to some other part of the environment quickly when necessary. A number of theorists have postulated cognitive control functions that are responsible for these abilities, and several have suggested that the prefrontal cortex (PFC) plays a critical role [2,29,32,47,50]. Our study focuses on the role of the lateral PFC in two specific types of cognitive control—processing selection and attentional set shifting. Processing selection regulates the flow of information through the system, selecting inputs so that the brain focuses on relevant information and filters out irrelevant information [38]. Set shifting switches the state of the information processing system from one mode of processing to another, or it shifts the focus of attention from one attribute of a stimulus to another (see Ref. [34] for a review).

1.1. The cognitive control of set shifting

At a computational level, we consider 'set-shifting' to include all those processes that change the mapping between stimulus attributes and response attributes. The types of computations thought to underlie set shifting have been explored in two lines of research, one concerned with switching from one task to another, and another concerned with attention switching. The task-switching literature derives from the numerous studies of frontal lobe function revealing that the PFC is critical for switching from one

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task to another. The classic example is the difficulty that individuals with prefrontal damage have performing the Wisconsin Card Sorting Test. In that task, subjects sort a pack of cards according to particular rules (e.g. by shape or by color). Compared with controls, individuals with prefrontal damage perseverate—continue with incorrect sorting strategies—when the rule changes and error feedback is given [33].

A number of studies have shown that prefrontal damage affects performance in experimental situations where individuals must change from performing one task to some other task. Because the studies involved lesions with variable loci and etiologies, however, it is unclear to what extent the lateral PFC is critical for switching performance. Owen et al. [36,37] found that individuals with prefrontal damage were impaired when switching between a task requiring attention to one dimension of the stimulus (e.g. shape) and a task requiring attention to some other dimension (e.g. color). Within-dimension switches (e.g. between one color and another) did not produce significant impairments. In both studies, the group with prefrontal damage included individuals with damage to orbital and medial frontal areas as well as to lateral areas.

Rubinstein et al. [45] found that an individual with left-sided dorsolateral prefrontal damage showed poorer switching performance than individuals with other prefrontal lesions and controls (comparing the reaction times in blocks with switch trials to blocks with no switches). Rogers and colleagues [43] found that individuals with damage to the left PFC exhibited significant switch costs relative to controls. Individuals with damage to the right PFC did not show such a deficit. The prefrontal lesions in the group included medial and orbital frontal cortex as well as lateral areas, and thus it is unclear what the relative contribution of lateral frontal areas was.

Neuroimaging supports the involvement of lateral prefrontal regions in task switching. A positron emission tomography (PET) study compared PET activation during blocks of trials in which switches were required to activation when switches were not required [31]. Task switches activated left lateral regions only when the task involved a switch between stimulus dimensions (as in the Owen et al. studies described above). Within-dimension task switches did not activate these left regions. Rogers and colleagues found a similar dissociation using PET activation recorded during performance of a task involving feedback-induced switches [42]. Other functional magnetic resonance imaging (fMRI) evidence supports lateral prefrontal involvement, although there is some debate about whether the involvement reflects new areas specific to control or additional activity in the same areas used for single-task performance [1,6,15].

At a more basic level, a task switch includes a change in the focus of attention from one attribute of a stimulus representation to another [46]. Although a switch can require changing the focus of attention from one dimension (e.g. color) to another (e.g. shape), attentional switches can also involve a within-dimension shift, such as an attentional shift from the color red to the color green. A major line of research relevant to such intra-dimensional shifts is the research concerning covert shifts of visuospatial attention [40,41]. Most of these studies have used the Posner precuing paradigm, in which stimuli appearing in advance of a stimulus inform the subject of the likely location of the upcoming stimulus, allowing the attentional spotlight to move covertly (unaccompanied by eye movements) to that location before the stimulus appears [40,41].

Evidence from these studies is consistent in showing the involvement of parietal regions in visuospatial attention shifting [13,41]. More recent evidence, however, suggests that lateral frontal structures may also be important. For example, Hopfinger and colleagues [23], using event-related fMRI, found that the superior frontal gyri bilaterally, and the left-hemisphere middle frontal gyrus, were activated in response to cues that directed attention to lateral locations. Other studies using blocked designs have reported activity associated with switching in the right lateral prefrontal, bilateral premotor (frontal eye field), and in some individuals more inferior frontal regions [20,35,44].

Considered together, the studies of task switching and attentional switching present a puzzling contradiction. Those task-switching studies that have examined intra-dimensional switches suggest that the prefrontal cortex is not necessary to switch attention within a stimulus dimension. Studies focusing on more basic shifts of covert visual attention, however, have found evidence of lateral prefrontal involvement. One aim of our study was to explore the possible role of the lateral PFC in non-spatial shifts of visual attention.

1.2. The cognitive control of processing selection

Another type of top-down control is necessary to focus processing on relevant information and to filter out distracting, irrelevant information. These have been labeled ‘processing selection’ [38,52] or ‘attentional selection’ [3] functions. Studies commonly assess processing selection using variants of the Stroop task (see Ref. [30] for a review) and Eriksen flanker task [17], both of which involve irrelevant attributes of the stimulus signaling an incorrect response, causing elevated reaction times (RTs) and error rates [12]. The increase in RT and error rate caused by the irrelevant attributes indexes the limits of the processing selection mechanisms.

Although the literature often assumes a well-established association between prefrontal function and performance on these tasks [10], direct evidence from lesion studies is surprisingly sparse and somewhat contradictory. Perret [39] found that individuals with left-hemisphere frontal lobe lesions had elevated Stroop RT effects, compared with other lesion groups and healthy controls. Perret did not report error rates. Vendrell et al. [54] found that

damage to the right lateral PFC was associated with elevated Stroop effects on error rates and not RT. Most recently, Stuss and colleagues reported a group of individuals with lateral prefrontal damage whose difficulty with Stroop performance was in naming colors, not in the interference created by the word [51]. Several methodological points may have caused these discrepancies, particularly the heterogeneity of the subject groups. In the Perret and Vendrell studies, the groups included a large number of tumors with mixed dorsolateral, orbitofrontal, and mesial frontal pathology. In the Stuss et al. study, the cause of the injuries included stroke, hemorrhage, tumor, and head injury. Moreover, testing was performed prior to surgery in the Perret study and after the injury in the Vendrell et al. and Stuss et al. studies.

A growing body of neuroimaging evidence supports the involvement of lateral PFC in the performance of Stroop-like tasks. PET experiments have found activation of the left inferior frontal gyrus associated with Stroop interference [52,53]. An fMRI study of a Stroop-like task requiring numerosity judgments found activation in the left and right middle frontal gyri that differentiated neutral from interference blocks [7]. A number of fMRI studies of variants of the Stroop task confirm the presence of lateral prefrontal involvement, including inferior and middle frontal gyri [3,4]. Another study found PET activation in the left inferior frontal gyrus in an item recognition task where the items had been associated with a response that was no longer correct [24]. Much like a Stroop task, the item-recognition task required subjects to filter out irrelevant information.

1.3. The present study

Our study sought to clarify the role of the lateral PFC in processing selection and attention switching. Our approach was to administer a task that required both of these functions to a group of individuals with focal, unilateral lesions with a common etiology. Subjects performed a letter discrimination task, in which they made a squeezing response to a target letter with one hand if the letter was ‘H’ and with the other hand if the letter was ‘S’. Fig. 1 shows the sequence of stimuli in the task. The target letter was one of two letters that appeared on each trial, with one letter appearing in green and the other in red. That letter pair was preceded by a precue indicating which letter in the pair was the target letter. The precue was the word ‘red’ or ‘green.’ Thus, if the precue was the word ‘red’, then the red letter in the subsequent pair would be the target letter, to which the participant must respond. The other (in this case green) letter would be a distractor letter, with successful performance depending on ignoring the identity of the distractor letter.

Two manipulations were the central focus. First, on

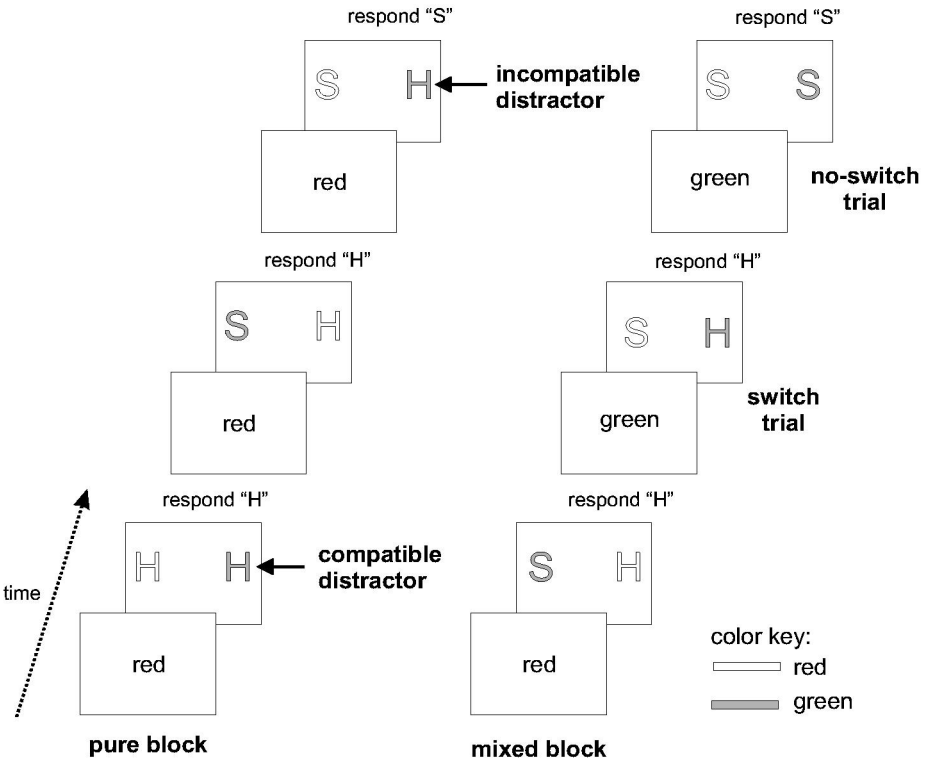

Fig. 1. The experimental task, depicted with the first in a sequence of screen images at the bottom of the figure and the last in the sequence at the top. For letters, the color green is depicted as gray, and the color red is depicted as white (see key). The left side of the figure depicts the sequence of events from a series of three trials in a pure no-switch block. The right side of the figure represents trials from the mixed switch/no-switch block. Note that within the mixed condition, the second trial constitutes a switch from the first trial, whereas the third trial does not require a switch from the second trial.

some blocks of trials (*pure condition*), the precue was always the same word. Thus, the participant could maintain attention to a particular color from one trial to the next. On other blocks of trials (*mixed condition*), the precue changed randomly from trial to trial. In these blocks, subjects frequently had to change their attentional set. We assessed the costs involved in switching attentional sets in two ways. First, we compared performance on no-switch trials in the mixed condition to performance in the pure condition. Because both are no-switch trials, the reaction time effect will not include the time it takes to switch attention per se. Instead, the pure versus mixed comparison can reflect costs related to the need to coordinate and maintain two attentional sets, the time required to process the precue stimulus, and possibly other strategic adjustments. Second, within the mixed condition, we compared performance on trials that required a switch from the previous attentional set (target color) to trials where no switch was required. This comparison should more directly reflect the time it takes to switch attention from one color to another. If prefrontal damage impairs the ability to switch attentional sets, individuals with such damage should show greater performance costs than controls in one or both of the comparisons. The pattern of impairments across comparisons will help in identifying the processes that are impaired.

The second manipulation was distractor compatibility, a version of the flanker compatibility manipulation of Eriksen and Eriksen [17]. On half of the trials (*compatible condition*), the identity of the irrelevant distractor letter was identical to the target letter (an H accompanying a target letter H, or an S accompanying a target letter S). On the other trials (*incompatible condition*), the distractor had the opposite identity from the target letter (an S accompanying the target letter H, or an H accompanying the target letter S). To examine the effects of prefrontal damage on processing selection, we compared compatible and incompatible trials. On incompatible trials it is particularly important that the subject attends only to the target letter and not to the distractor letter. Presumably, if prefrontal damage impairs processing selection, larger costs in RT and accuracy would be observed on incompatible trials for individuals with prefrontal damage.

2. Method

2.1. Subjects

The PFC lesion group consisted of six individuals (four men and two women, mean age 69) for whom computerized tomography (CT) or magnetic resonance imaging (MRI) evidence showed a lesion centered in the lateral PFC, resulting from infarction of the middle cerebral artery (Fig. 2). All subjects were at least 1 year post-lesion. The Brodmann areas affected in each individual were as follows. AL: areas 4, 6, 8, 9, 46, 44, 45, 46 anterior 22; JD: areas 6, 9, 44, 45, 46, 47; RT: areas 6, 9, 44, 45, 46; OA: areas 6, 44, 45, 46; EB: areas 44, 45, 46; MM: areas 6, 8, 9, 10, 44, 45, 46, 47. The area of maximal lesion overlap among the six individuals was in the ventrolateral prefrontal cortex centered in areas 44 and 45 of the inferior frontal gyrus and posterior portions of area 46 in the middle frontal gyrus. As a control, three men (mean age 74) were selected based on evidence that they had lesions in the posterior association cortex. Brodmann areas affected in these individuals were: HT: areas 19, posterior 39; LP: areas 7, 19; RW areas 7, 19, 39, 40. All prefrontal and parietal lesions resulted from infarction of the middle cerebral artery. A group of older adults (four males, six females, mean age 70) matched in mean age to the prefrontal group, and a group of young adults (four males, six females, mean age 24) served as neurologically healthy controls. All subjects were paid $10.00 per h. The study was approved by the Institutional Review Boards of the Martinez Veterans Administration Medical Center and the University of California.

2.2. Stimuli

Stimuli were presented on an NEC 5FGe 21-inch color monitor. On each trial, the participant was presented with two letters, one printed in red and the other printed in green, which remained on the screen until the response (Fig. 1). At a viewing distance of 1.5 m, each letter subtended a visual angle of approximately 1°. One was presented 2° to the left of fixation, and the other appeared 2° to the right. One letter appeared in red and the other appeared in green. Four letter pairs (HH, HS, SH, and SS) were possible; with the color combinations (red left/green right or red right/green left), there were eight possible imperative stimuli. The precue consisted of the word ‘red’ or ‘green’ in lowercase letters. On every trial, the onset of the precue (duration 200 ms) preceded the onset of the imperative stimulus by 1000 ms. Each precue occurred at a randomly selected interval of 1000 or 2000 ms after the response on the previous trial. A fixation point (‘+’) subtending 0.15° of visual angle appeared in the center of the screen and remained visible throughout the block of trials.

2.3. Responses

The subjects responded by squeezing devices (one for each hand) consisting of a hand grip attached via a spring to a force transducer. The force transducers were 20 lb capacity thin beam load cells (Omega Engineering, LCL-020). The hands were positioned with the palm facing downward and the fingers resting on a horizontal bar attached to a vertical platform. The squeezing movement consisted of flexion of the fingers, starting with the fingers fully extended, which moved the horizontal bar, rotating the platform. The transducer transformed the force applied to it into a voltage, which was digitized continuously at

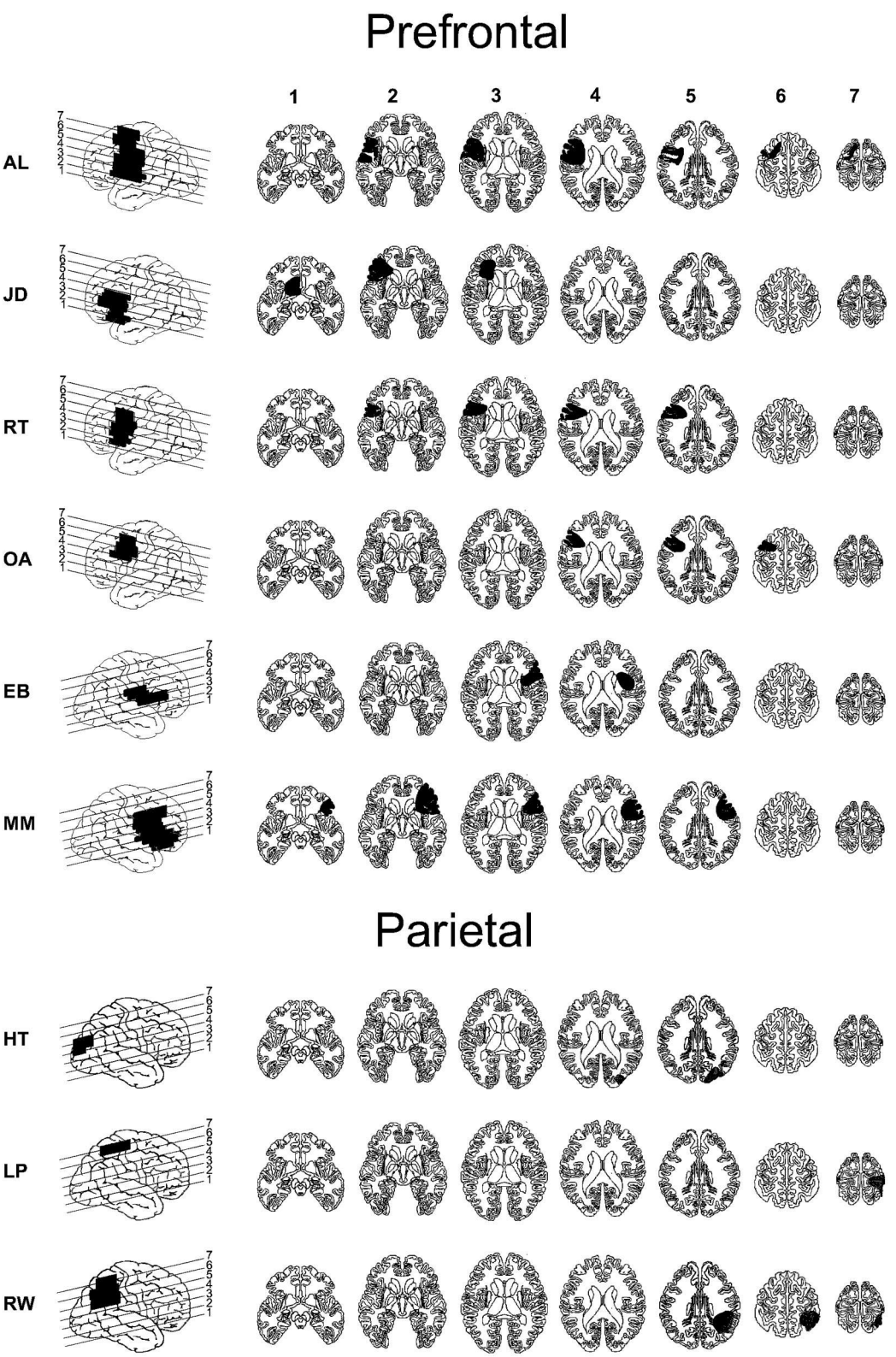

Fig. 2. Lesion reconstructions in the six individuals with unilateral damage in the lateral prefrontal cortex and the three with right parietal damage. The shaded areas show the extent of the lesion. The lines on the lateral reconstructions indicate the location of the corresponding axial section.

800 Hz. (EEG recordings were also made for the purpose of another study [19].) A mercury switch on the platform closed when the bar moved 3 cm.

The RT was defined as the interval between the onset of the target stimulus and the switch closure. For each participant, a criterion consisting of the mean RT plus 2.5 standard deviations was computed, and any responses earlier than 50 ms or later than that criterion were excluded

from analysis. For comparison with previous research [18], the moment of squeeze onset was also determined. First, the standard deviation of the force transducer output during the period from 200 ms prior to the warning stimulus to the time of the imperative stimulus was computed. A threshold value was set at 2.5 times this baseline standard deviation value. An algorithm then identified the squeeze onset as the point following the imperative stimulus (and prior to the next trial) at which the transducer output crossed this threshold. For the analyses reported below, we report the RT as measured by switch closure. The squeeze onset measure yielded results that were qualitatively the same.

2.4. Procedure

On each trial, the participant was presented with two letters, one printed in red and the other printed in green (Fig. 1). One of these was the target letter, and the participant had to make a speeded response according to the identity ('H' or 'S') of the target letter. A precue (the word 'red' or 'green') designated which letter of the letter pair was the target letter. If the precue was the word 'red', then the red letter was the target letter; if the precue was 'green', then the green letter was the target. The participant had to squeeze one response device if the target letter was 'H' and the other device if the target letter was 'S.'

In the *mixed* condition, the precue (and thus the relevant color) varied randomly on a trial-to-trial basis. In this condition, trials that called for a switch from the previous trial's attentional set were called *switch* trials. Those where no switch was required were *no-switch* trials. In the *pure* condition, the precue was always 'red' or always 'green,' and thus all trials were no-switch trials. Each target letter was accompanied by an irrelevant distractor letter that had the same identity as the target letter (HH or SS; *compatible* condition) or had the opposite identity (HS or SH; *incompatible* condition). Half the trials were compatible, and half were incompatible. Each participant completed 16 blocks of 32 trials—eight mixed blocks and eight pure blocks. Mixed and pure blocks were presented in eight pairs: within each pair, the order was determined randomly. Within each block, there were four repetitions of each of the eight possible imperative stimuli. In mixed blocks, 16 of the precues were the word 'red' and 16 were the word 'green.' In pure blocks, all precue stimuli were the same word, with four blocks of 'red' and four blocks of 'green'. Hand assignment was counterbalanced.

3. Results

The results section is divided into several parts. Because the study used a novel task, our strategy was first to examine the effects of the task manipulations on the behavior of young, neurologically healthy adults, to confirm that the manipulations had the anticipated effects on RT. We then compared the PFC group and the age-matched control group, to test for the effect of PFC damage on attention switching and processing selection. The effects of switching can appear in this task in two ways: either as a difference between pure and mixed blocks, or as a difference within the mixed block, between switch and no-switch trials. Each of the analyses therefore consisted of two parts. First, we compared the no-switch trial RTs from the pure no-switch blocks to those from the mixed blocks. We then focused on the mixed blocks, comparing the no-switch trial responses in those blocks to the switch trial responses. In preliminary analyses, we determined that the effects of factors such as the laterality of targets and distractors, hand of response, and color of the stimulus did not differ between the groups; we therefore restricted the analysis to the distractor compatibility and switching manipulations. Unless otherwise noted, the analysis consisted of a 2 (group) $\times$ 2 (switch effect) $\times$ 2 (distractor compatibility) ANOVA for the PFC versus control comparison, and a 2 (switch effect) $\times$ 2 (distractor compatibility) ANOVA for the young subjects. For the PFC versus control group analyses, we do not report most main effects if they were superseded by interactions with the group factor.

3.1. Analysis of no-switch trials in pure versus mixed blocks

The attention switching and distractor compatibility manipulations caused performance costs in the form of increases in RT and decreases in accuracy. Fig. 3 shows the RT means for the young subjects in the comparison of no-switch trials from pure blocks versus no-switch trials in mixed blocks. As the graph suggests, no-switch trial responses were slower in the mixed blocks than in the pure no-switch blocks, $F(1, 9)=45.16$, $P=0.000087$, $MSe=181$. Responses were slower when the distractor letter was incompatible with the response than when it was compatible, $F(1, 9)=47.90$, $P=0.000069$, $MSe=345$. The switch and compatibility manipulations did not interact, $F(1, 9)=1.28$, $P=0.287$, $MSe=64$. Accuracy data (proportion correct) were consistent with the RTs. Subjects performed less accurately on no-switch trials in mixed blocks (0.90) than in pure blocks (0.91), $F(1, 9)=6.76$, $P=0.029$, $MSe=0.0032$. (Proportion correct data were analyzed with the arc sine transform.) Responses were less accurate on incompatible distractor trials (0.88) than on compatible trials (0.93), $F(1, 9)=11.75$, $P=0.0075$, $MSe=0.0165$.

The corresponding RT data for the PFC group and the age-matched controls are shown in Fig. 4. Of most interest, the increase in RT on incompatible trials relative to compatible trials was greater in the PFC group than in the control group, $F(1, 14)=6.26$, $P=0.025$, $MSe=10\,707$. The PFC group was slower overall than the control group, $F(1, 14)=13.71$, $P=0.0024$, $MSe=666$. As in the previous

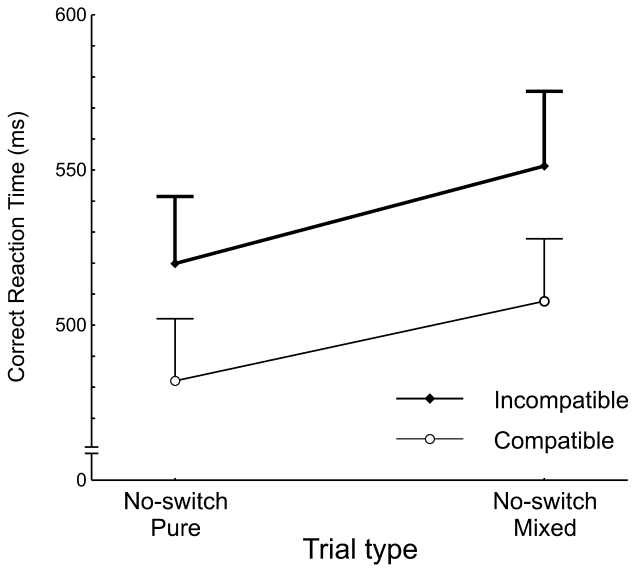

Fig. 3. Correct reaction times for the young subjects, in the comparison of no-switch trials from pure no-switch blocks versus those from mixed blocks (mixtures of switch and no-switch trials). Filled diamonds and thick lines represent incompatible distractor trials. Open circles and thin lines represent compatible distractor trials. Error bars are +1 standard error.

analysis, no-switch trial responses were slower in the mixed blocks than in the pure blocks, $F(1, 14)=25.06$, $P=0.00019$, $MSe=2973$. The effect did not differ between groups, $F=0.66$. Interestingly, unlike the analysis of the young subjects alone, the effect of block interacted with compatibility, $F(1, 14)=5.86$, $P=0.030$, with a larger compatibility effect in mixed blocks than in pure blocks. The group×block and group×compatibility×block interactions were not significant, $F=0.57$ and $F=0.90$, respectively. Group effects on accuracy were not evident. Subjects were less accurate on incompatible trials (0.91) than on compatible trials (0.96), $F(1, 14)=6.68$, $P=0.022$, $MSe=0.068$. The difference between the mixed-block (0.93) and pure (0.94) no-switch accuracy was not significant, $F=0.79$.

3.2. Analysis of mixed-block switch versus no-switch trials

The within-block analysis consisted of a comparison of switch trial and no-switch trial performance from the mixed blocks. For the young subjects (Fig. 5), switch trial responses (530 ms) were not significantly slower than no-switch trial responses (535 ms), $F(1, 9)=1.39$, $P=0.27$, $MSe=215$. Analysis of accuracy also revealed no significant effect of switching, $F=0.37$. RTs on incompatible distractor trials were greater than on compatible trials, $F(1, 9)=39.39$, $P=0.00029$, $MSe=525$. The difference in accuracy between compatible (0.92) and incompatible (0.87) trials did not reach significance, $F(1, 9)=3.73$, $P=0.086$, $MSe=0.045$.

As in the previous analysis, a salient difference between

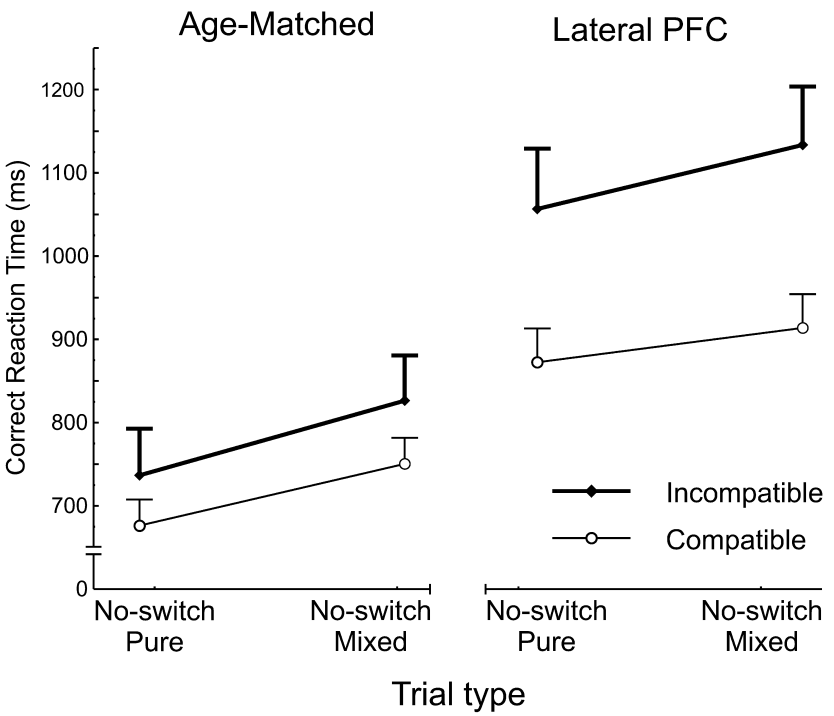

Fig. 4. Correct reaction times for the subjects with damage to the lateral prefrontal cortex (PFC) and the age-matched control group, comparing no-switch trials from pure no-switch blocks versus those from mixed blocks (mixtures of switch and no-switch trials). Filled diamonds and thick lines represent incompatible distractor trials. Open circles and thin lines represent compatible distractor trials. Error bars are +1 standard error. Relative to control subjects, the PFC group showed an increased compatibility effect but an equivalent switching effect.

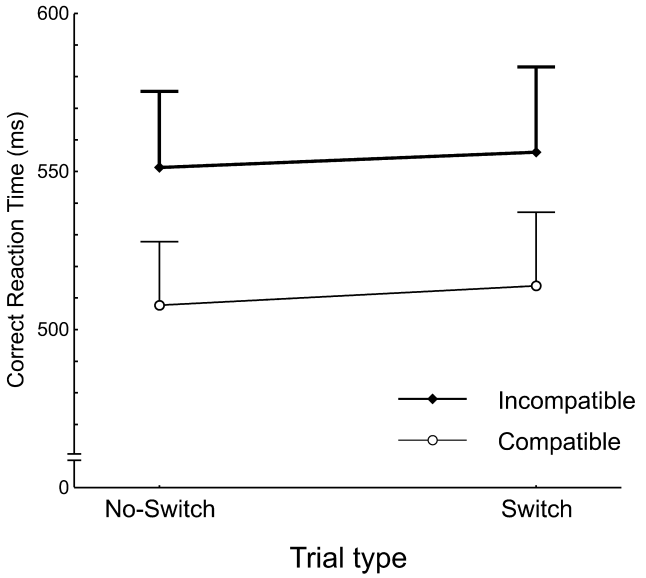

Fig. 5. Correct reaction times from the switch (mixed) blocks, for the young subjects. The abscissa corresponds to the comparison of no-switch trials and switch trials. Error bars are +1 standard error. Filled diamonds/thick lines represent incompatible distractor trials. Open circle/thin lines represent compatible distractor trials.

groups was the response to distractor compatibility (Fig. 6). The distractor compatibility effect was larger in the PFC group than in the control group, $F(1, 14)=6.10$, $P=0.027$, $MSe=10\,283$. In contrast to the young controls, the age-matched control and PFC groups responded more slowly on switch trials than on no-switch trials, $F(1, 14)=13.13$, $P=0.0028$, $MSe=3133$, but the effect did not differ between groups, $F=0.57$. The PFC group was slower than the control group, $F(1, 14)=13.34$, $P=0.0028$, $MSe=3133$. The two groups responded less accurately on switch trials (0.90) than on no-switch trials (0.93), $F(1, 14)=12.87$, $P=0.0030$, $MSe=0.020$. They were also less accurate on incompatible trials (0.88) than on compatible trials (0.95), $F(1, 14)=12.23$, $P=0.0036$, $MSe=0.075$.

3.3. Correction for slowing

The analyses described above suggest that the PFC group showed a larger compatibility effect than the age-matched control group. Nevertheless, the individuals with PFC damage were slower than the age-matched control group, and it is possible that the compatibility effect, as a proportion of overall RT, was the same in the two groups. We carried out an additional analysis on the compatibility effect to correct for this overall slowing. We computed a corrected RT measure consisting of the compatibility effect (mean incompatible RT-mean compatible RT) divided by the overall mean RT. We then carried out a one-way analysis of variance comparing the two groups on this ratio. This corrected measure of the compatibility effect was larger in the individuals with prefrontal damage (0.179) than in the age-matched controls (0.093), $F(2, 23)=4.10$, $P=0.030$, $MSe=0.005$. We performed a similar analysis on the corrected between- and within-block

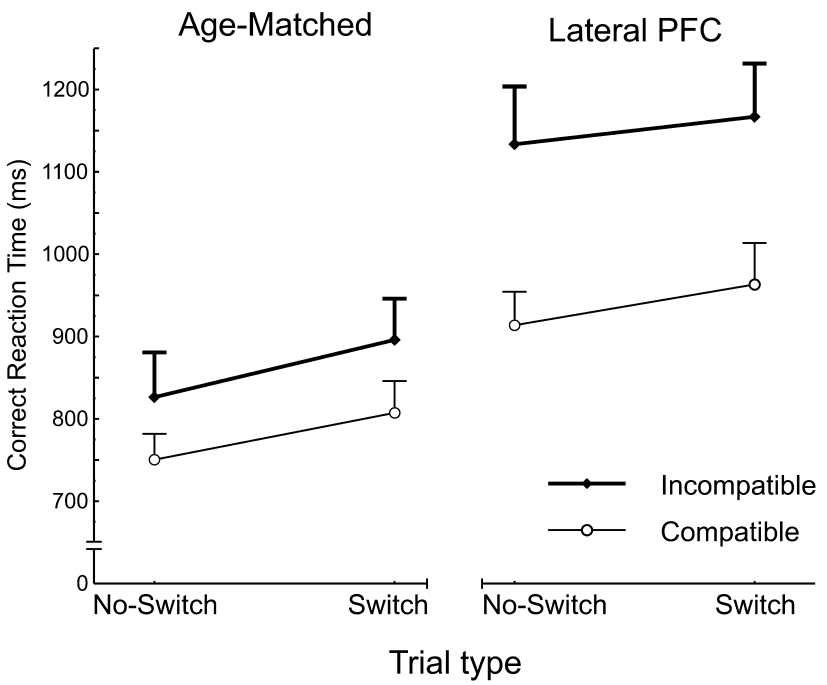

Fig. 6. Correct reaction times from the switch (mixed) blocks, for the subjects with damage to the lateral prefrontal cortex (PFC) and the age-matched control group. The abscissa corresponds to the comparison of switch and no-switch trials. Filled diamonds and thick lines represent incompatible distractor trials. Open circles and thin lines represent compatible distractor trials. Error bars are +1 standard error. Relative to control subjects, the PFC group showed an increased compatibility effect but an equivalent switching effect.

switching effects. Neither group difference was significant (between block, $F(1, 14)=3.08$, $P=0.10$, $MSe=0.072$; within block, $F(1, 14)=1.19$, $P=0.29$, $MSe=0.003$).

3.4. Individual differences

For a more detailed analysis of these data, we focused on data of individual subjects. A number of individual differences could be blurred by the grouping categories. For example, even within the prefrontal group, the lesion locations and sizes were not homogeneous. Also, three individuals with parietal damage participated, and analyzing their individual data allowed us to determine whether damage to posterior regions could influence processing selection or attention switching.

To analyze the compatibility effect for individual subjects, we computed a 95% confidence interval for the age-matched controls' individual performance. We did this for two measures, the raw compatibility effect and the corrected compatibility effect. Individuals whose performance fell outside of this interval can be considered significantly impaired relative to the control group. Table 1 shows the individual subjects' data, denoting which subjects exceeded the confidence intervals for the raw and corrected compatibility effects. Three individuals with prefrontal damage (AL, RT, and JD) exceed the age-matched controls' 95% confidence interval for the distractor compatibility effect, both for the raw and for the corrected measure. One of the individuals (JW) with parietal damage exceeded the 95% confidence interval for the raw compatibility effect but not for the corrected effect.

Analysis of the pure versus mixed and no-switch versus switch measures of attention switching revealed no patients with prefrontal damage whose switching effect exceeded the 95% confidence interval for the age-matched control group. We did observe, however, some cases in which switching times were unusually fast (Table 1). JD's within-block switch effect values, RT's between-block switch effect values, and RW's corrected within-block switch effects all fell below the 95% confidence interval for the age-matched control group. One individual, HT, with a right posterior lesion, showed an exaggerated switching effect in the analysis of no-switch versus switch trials.

4. Discussion

The performance of the individuals with prefrontal damage in this study augments the findings of other studies of processing selection and set shifting. The experimental task elicited switching effects and compatibility effects from the young and older control subjects, validating its use in examining processing selection and attention switching. The within-block switching effect was not statistically significant in the younger subjects, however, which may indicate that the 1-s SOA gave those subjects enough time to perceive the precue and make the attentional switch before the target stimulus appeared.

The finding that prefrontal damage failed to affect switching performance meshes with findings from other studies that have failed to find significant effects of

Table 1
Analysis of individual subjects' performance

Subjects	Mean RT (ms)	Compatibility effect (S.D.)		Between-block switch effect (S.D.)		Within-block switch effect (S.D.)	
		Raw (ms)	Corrected	Raw (ms)	Corrected	Raw (ms)	Corrected
Young controls	517	40.8 (17.7)	0.078 (0.031)	31.6 (17.7)	0.060 (0.032)	5.5 (14.7)	0.008 (0.027)
Age-matched controls	765	69.3 (34.0)	0.093 (0.053)	116 (60.9)	0.150 (0.073)	63.2 (42.0)	0.074 (0.048)
AL	1139	271*	0.238*	57	0.050	30.5	0.026
JD	1131	393*	0.347*	79	0.070	−90.3†	−0.077†
RT	1214	342*	0.282*	−6.0†	−0.005†	68.9	0.057
OA	814	92	0.112	147	0.180	75.6	0.084
EB	994	40	0.041	152	0.153	133.4	0.125
MM	734	40	0.054	46	0.062	30.9	0.041
HT	1096	25	0.023	199	0.181	209.2*	0.175*
LP	774	73	0.094	72	0.093	15.8	0.019
RW	1439	210*	0.146	209	0.145	−131.4	−0.085†

Note. Data from individual subjects with brain injuries, with group data from the young and age-matched control groups. Lesion locations are depicted in Fig. 1. The compatibility effect represents the mean compatible RT subtracted from the mean incompatible RT. The between-block switch effect is the mean RT on no-switch trials in pure no-switch blocks subtracted from the mean RT on no-switch trials in mixed blocks (blocks with both switch and no-switch trials). The within-block switch effect is the mean RT on no-switch trials in mixed blocks subtracted form the mean RT on switch trials. The standard deviations (S.D.) are in parentheses. The raw values represent the actual RTs in ms, the corrected values correct for slowing by dividing the raw values by the corresponding mean RT.

*Exceed the 95% confidence interval for individuals' performance (mean+1.96 S.D.), derived from the age-matched control group data.

†Fall below the corresponding 95% confidence interval.

prefrontal damage on the switching of attention between attributes of the same perceptual dimension (e.g. switching attention from one color to another, from one shape to another, etc.) [36,37]. Studies have more consistently found switches from one perceptual dimension to another (e.g. from shape to color, from color to numerosity, etc.) to be influenced by prefrontal damage [36,37] or to be associated with activity in prefrontal regions [31,42]. Similar findings have been reported in individuals with Parkinson's disease [21,36,37]. This result suggests that the shifts of visuospatial attention reflect a different mechanism than the one required for shifting in our task [23]. It is important to note, however, that the lesions in our subject group may have failed to damage the areas showing activation in neuroimaging studies. Compared with the lesions in our group, those regions have tended to be more superior [14,23,44] or in the right hemisphere [13].

Although there were no significant differences between the PFC and control groups in switching effects, a few details prevent one from concluding that the PFC is in all cases unrelated to between- or within-block switching performance. In particular, two individuals with PFC damage (RT and JD) showed reduced switching effects relative to the age-matched controls. These two individuals also showed significantly lengthened compatibility effects, and thus one possible explanation for the reduced switching effects is a strategic adjustment associated with lengthened compatibility effects. Supporting such a possibility, the pattern of reduced effects in these two individuals is unusual: in both cases the pattern appears as a reversal in the switching effect. An unusual response strategy could cause a reversal: responding more conservatively in the no-switch blocks than the switch blocks, for example, would cause such a reversal. Within the switch blocks, a response strategy favoring alternations over repetitions could also cause a reversal in the switch effect. Nevertheless, such explanations must be considered speculative, and additional work will be necessary to determine whether PFC damage can reduce the costs associated with attentional switching.

Coupled with the switching results, the enhancement of the distractor compatibility effect in the PFC group suggests that the PFC contributes to attentional selection operations that are distinct from the operations needed to shift attention. None of the individuals in the PFC group showed an increase in both the distractor compatibility and the switching effects. Because the distractor compatibility and pure versus mixed switch effect had additive effects on RT, the evidence is especially strong that the processes giving rise to those two effects are temporally and functionally distinct [49]. It is interesting that an individual with right parietal damage showed elevated switching effects, because the right parietal lobe has been implicated in the switching of attention [23,28,41]. It is also noteworthy that the significant effects in that patient, relative to controls, were observed in the within-block comparison, which should be most sensitive to the operations that switch attention from one trial to the next. If these data were to be observed in a larger sample of individuals, the double dissociation would solidify the evidence for a functional distinction between attention switching and processing selection.

Analyzing the interference effect in the individual subjects shed light on the localization and cause of that effect. Those individuals with prefrontal damage whose data showed elevated distractor compatibility effects—AL, RT and JD—are noteworthy for two reasons. First, they all had lesions in the left posterior inferior prefrontal cortex. Two individuals with right-sided lesions and one with a more superior left-sided lesion failed to show compatibility effects that differed from controls. Second, the lesions in those three subjects tended to be larger than the rest of the PFC group. It does not appear, however, that lesion size alone can account for the findings: the largest of the lesions among those showing elevated compatibility effects (AL) is approximately the same size as the lesion of one of the other subjects (MM) who did not show an elevated compatibility effect. The data therefore suggest that left-sided, relatively inferior and posterior regions are particularly critical for processing selection.

Our data are consistent with the proposals of a number of investigators in which the PFC regulates attention via top-down control of other brain regions [3,4,16,25,27, 32,48]. The elevated distractor compatibility effect in the PFC group is consistent with other studies showing lateral prefrontal involvement in the Stroop task and Stroop-like tasks [38,52–54]. Our study extends this literature to include tasks such as the Eriksen task (see also Ref. [22]). The results suggest the left lateral PFC, possibly a relatively inferior region, is most critical for modulating the effects of distracting inputs. Note, however, that the linguistic nature of the stimuli could have contributed to that particular localization result, and that a right hemisphere locus might be important for other types of stimuli [22].

The effect of PFC damage on processing selection and the lack of such an effect on attention switching contrasts with the evidence reviewed earlier that prefrontal damage impairs between-dimension attentional selection and switching [26]. Task differences may underlie the divergent results: In the Eriksen task and the present study, attention must perform its selection within a perceptual dimension—in the Eriksen task it is the spatial dimension, and in our task it is the dimension of color. In the Stroop task, however, selection occurs between dimensions: one must select color and ignore the word, for example. As our study and the studies reviewed in the introduction have shown, the PFC is necessary in both types of tasks for overcoming interference. In a similar fashion, switching in our task is within a dimension, and in more complex tasks the switching occurs between dimensions [31,36,42]. Why

then is switching only dependent on the PFC in the between-dimension switching tasks, and not in the within-dimension tasks?

Models of visual attention and prefrontal function offer some insight into an answer to this question, suggesting an architectural reason that between- and within-dimensional selection and switching tasks might be affected differently by prefrontal damage. Cohen and colleagues have constructed a parallel-distributed processing model of prefrontal function that accounts for performance in tasks like the Stroop and Eriksen flanker task [5,9,11]. In the model of Stroop performance [9], a layer of task demand units biases the activation of two groups of units in the input layer, one corresponding to ink color, and one corresponding to the word name. Each group of units consists of homologous units corresponding to the codes for the 'red' and 'green' inputs. These units all connect to appropriate 'red' or 'green' units in a response layer. Units within an input layer group are reciprocally inhibitory, but the input layer groups do not inhibit one another. The conflict or crosstalk between the codes associated with the two groups of units thus becomes evident further downstream, in the form of the simultaneous activation of mutually inhibiting response units [5].

The architecture of the model of the Eriksen task is similar: task-demand units bias the input units corresponding to certain regions of visual space [11]. Cohen et al. have proposed a similar model for the task used in the present paper [8]. In that model, the task demand units bias the activation within an input module to favor the units corresponding to the attended color and to suppress the unattended-color units [8]. These models are different from the model of the Stroop task in one key respect: conflict in the Eriksen task and in our task can arise at the level of the input layer. In the model of the Eriksen task, units in the input layer that correspond to relevant information and those that correspond to irrelevant information inhibit each other via mutually inhibitory connections. When two units are active, conflict will occur within the input layer. (Note that this point is not a focus of the modeling, cf. [11].)

The manner in which competition between input-layer units differs in the Stroop model and in the model of the Eriksen task gains some theoretical support from the model of selective attention proposed by Desimone and Duncan [16]. In their model, attentional selection is accomplished both by top-down control as well as by competition between neurons via mutually inhibitory connections. Most relevant to the present discussion, competition is greater when competing cells are closer. Within-dimension selection and switching, in the Eriksen task and its variants, would therefore be affected more by the mutually inhibitory connections between relevant and irrelevant neurons than would performance in the between-dimension tasks, such as the Stroop.

These principles thus suggest a means by which lateral prefrontal lesions can affect within- and between-dimension switches differently. In the within-dimension case, if irrelevant and relevant input units can compete, then top-down suppression of the newly-irrelevant units may not be necessary to create the new attentional set. Instead, a biasing signal that activates the newly-relevant unit, coupled with the input-level mutual inhibitory connections, will accomplish the switch. For between-dimensional switches, however, the lack of mutual inhibition between the representations of the irrelevant and relevant dimensions means that suppression of irrelevant input involved in switching requires an external, top-down signal, provided by the PFC.

Of course, as we pointed out, both between- and within-dimension selection tasks (i.e. Stroop and Eriksen tasks) produce enhanced interference effects in individuals with PFC damage. Unlike within-dimension switching, within-dimension selection may not be able to rely on bottom-up competition for selection activity. Instead, top-down selection may be necessary even when mutually inhibitory connections exist between the units corresponding to relevant and irrelevant information. One reason for this contrast between switching and selection mechanisms might be the need for sustained activity in maintaining the selective state [32]. The system may thus be limited in capacity but also efficient, invoking prefrontal control only when other, bottom-up means for accomplishing the necessary processing are not enough.

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