Dissociating Task-set Selection from Task-set Inhibition in the Prefrontal Cortex

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Abstract

■ Patients with focal lesions in the left (n = 7) and right (n = 4) prefrontal cortex were compared with controls (n = 16) in a task-switching experiment using four different, simple spatial tasks. Each of these tasks involved a left–right decision, either regarding an arrow, the word ''left'' or ''right,'' a circle position, or the direction of a moving line. We compared performance on trials that required rule switches versus rule repetitions (local switch costs) and we compared performance between blocks with bivalent stimuli (two dimensions present) and blocks with univalent stimuli (only one dimension present) to assess global switch costs. Patients with left prefrontal lesions, but not patients with right prefrontal lesions, exhibited increased costs on trials in which the relevant dimension switched (local switch costs), but also on no-switch trials with bivalent stimuli (global costs). We also assessed task-set inhibition in the form of the backward-inhibition effect [increased response times to recently abandoned tasks; Mayr, U., & Keele, S. Changing internal constraints on action: The role of backward inhibition. *Journal of Experimental Psychology: General, 129,* 4–26, 2000]. Although left frontal patients showed normal inhibition, right frontal patients showed no evidence for inhibition. These results suggest a neurocognitive dissociation between task-set selection and inhibition. ■

INTRODUCTION

The prefrontal cortex is associated with a variety of executive functions, including the ability to flexibly change cognitive configurations (task sets) to newly relevant task demands. Theoretically, there may be two different aspects to the process of establishing a task set. First, the relevant rules must be activated (e.g., Mayr & Kliegl, 2000, 2003; Rubinstein, Evans, & Meyer, 2001). Secondly, interference from competing task sets has to be minimized, possibly through a process of active inhibition (e.g., Mayr & Keele, 2000). The dissociation of these two functions has proven to be notoriously difficult (e.g., Kane, Bleckley, Conway, & Engle, 2001; Cohen & Dehaene, 1998).

Here, we establish this dissociation by testing patients with lesions in the left or right prefrontal cortex and control participants in a variant of the task-switching paradigm. Task-switching situations require subjects to respond to stimuli on the basis of frequently changing stimulus–response rules (e.g., ''task sets''; Meiran, 2000; Rogers & Monsell, 1995). Response-time (RT) costs that arise from demands of switching between task rules provide an indicator of task-set selection efficiency. Recent variants of the task-switching paradigm have been tailored to assess specific subcomponents of control, such as the inhibition of competing task rules (e.g., Mayr & Keele, 2000).

In the current paradigm, subjects had to select between four different, simple spatial response rules on a trial-by-trial basis (see Figure 1), pressing one of two keys on each trial depending on the value of the response-relevant dimension. The different relevant dimensions were the word ''left'' or ''right,'' a small circle appearing on the left or the right side, two dashed lines moving either leftwards or rightwards, and arrows pointing either to the left or to the right. In each display, up to two dimensions could be present (see Figure 1). A verbal cue presented above the stimulus ensemble signaled the response-relevant dimension for the trial. On each trial there was a 25% chance that the cued dimension remained the same as on the previous trial and a 75% chance it changed. The contrast between switch trials and repetition trials allowed us to assess local switch costs. In addition, we contrasted blocks with bivalent and univalent stimuli. Bivalent stimuli contained both a relevant and an irrelevant dimension (e.g., an arrow and a circle when the relevant dimension was ''arrow''), and therefore, required cue-based selection of the relevant set. In univalent stimuli, only the currently relevant dimension was present, and therefore, set selection could occur in a bottom-up manner. The comparison between these two block types allowed the assessment of ''global'' task-set selection costs (also referred to as ''mixing'' costs; Meiran, 2000). In order

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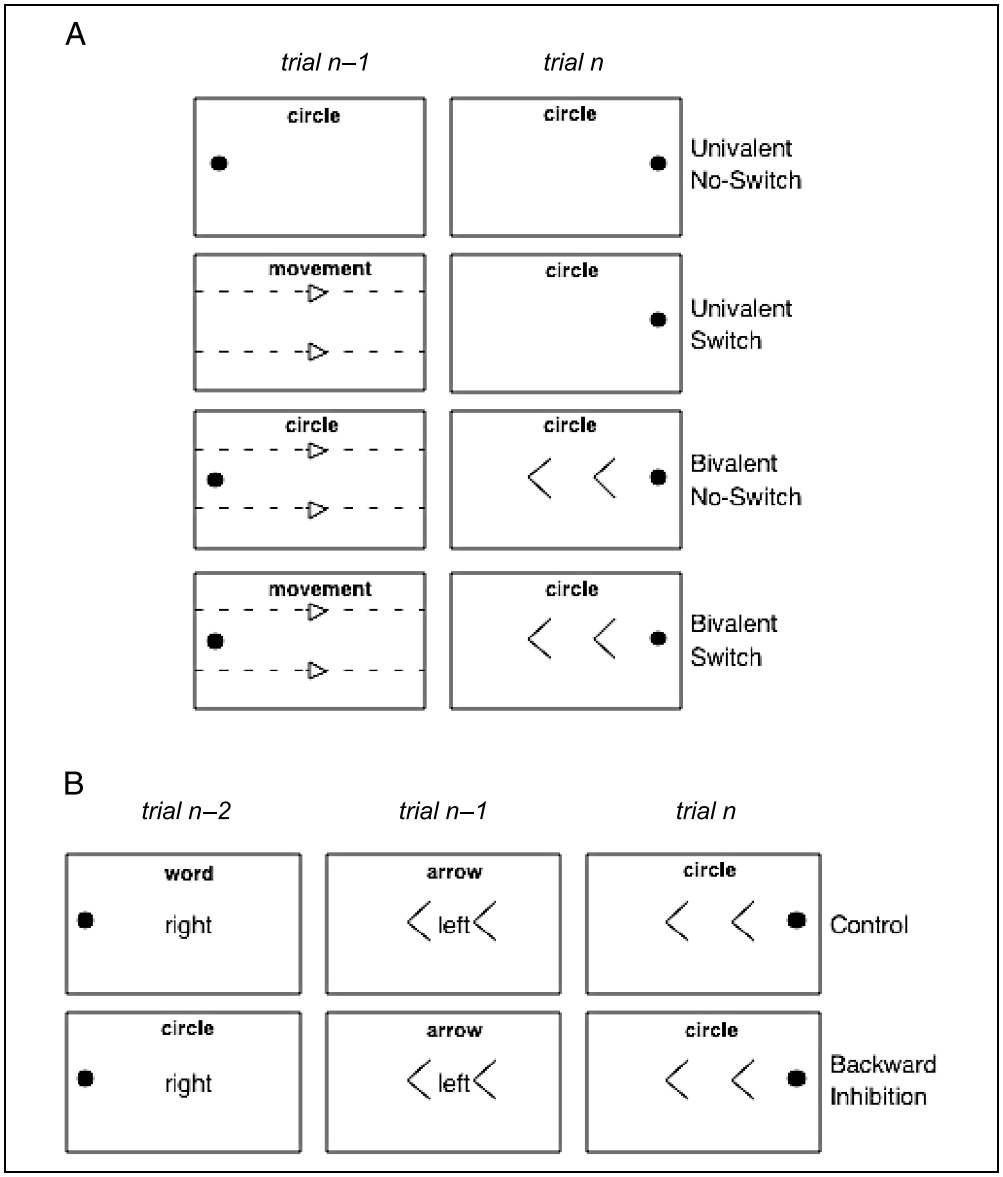

Figure 1. Main task-switching conditions. (A) Univalent no-switch, univalent switch, bivalent no-switch, and bivalent switch transitions. Local switch costs were defined as the difference between switch and no-switch trials. Global costs were defined as the difference between bivalent and univalent no-switch trials. (B) Trial transitions used to compute the backward-inhibition effect: Control (lag-2 task change) versus backward inhibition (lag-2 task repetition).

not to confound local and global switch costs, we only analyzed no-switch trials for this comparison. We also used single-task blocks with univalent stimuli in which the response-relevant dimension remained constant through the entire block (and thus, there was no need to switch task set). This condition served as a baseline that allowed us to control for group differences in general response speed.

A noteworthy feature of the current paradigm is the high frequency of task switches versus task repetitions (i.e., 75% vs. 25%). As will be described below, this was necessary to achieve a sufficient number of trial transitions diagnostic of task-set inhibition. However, a consequence of this design feature is that global costs (i.e., the difference between bivalent and univalent stimuli) are at least as critical in terms of indexing task-set selection demands as the local costs that serve as main dependent measure in traditional switching experiments. The reason is that in situations in which switch frequency is high and stimuli are bivalent, subjects come to expect a switch on every trial (e.g., Altmann, 2004; Mayr & Kliegl, 2000). Therefore, we will use both local and global costs as indicators of task-set selection efficiency.

Past work has shown that local, and sometimes also global, switch costs increase with left frontal insults (e.g., Keele & Rafal, 2000; Rogers et al., 1998). In addition, left frontal activity in brain imaging experiments has been associated with processing the task cue. Interestingly, in several studies, this left frontal cue-related activity has been found even on no-switch trials (Brass & von Cramon, 2002; MacDonald, Cohen, Stenger, & Carter, 2000). Accordingly, the first goal of the present study was to replicate the finding of a left frontal deficit in task-set selection as indicated through global or local costs.

The second goal was to examine the relationship between frontal deficits in task-set selection on the one hand, and task-set inhibition on the other. By some accounts, activation/retrieval of a task set and inhibition of task-set competitors are simply two sides of the same coin (e.g., Kimberg & Farah, 1993) and it is only through an active representation of the relevant information that irrelevant information can be suppressed. If this was the case, we should see indications of an inhibitory deficit in patients with a task-set selection deficit. However, if activation and inhibition are functionally distinct, then indicators of inhibition could be in the normal range, even in patients for which local and/or local switch costs indicate a set-selection deficit. The use of four different task sets allowed us to assess the so-called backward-inhibition effect, an established indicator of task-set suppression (Mayr & Keele, 2000; see also Schuch & Koch, 2003; Dreher & Berman, 2002; Mayr, 2001; Arbuthnott & Frank, 2000). This effect denotes an RT increase when switching to a recently abandoned and presumably still inhibited task compared to a switch that requires activating a less-recently relevant task. For example, switching to the arrow task in the triad circle–arrow–circle in Figure 1B may require inhibition of the circle task set, which in turn may lead to increased RT on the third trial of the triad when returning to the circle task (compared to the third trial of a control triad such as word–arrow–circle). The lingering effect of this inhibition is referred to as backward inhibition.

Although there is evidence of a left frontal set-selection deficit, there is also evidence that conflict on the level of responses or competing sets engages the right prefrontal cortex (e.g., Hazeltine, Poldrack, & Gabrieli, 2000; Garavan, Ross, & Stein, 1999; Konishi et al., 1999; see Aron, Robbins, & Poldrack, 2004, for a review). Even more to the point, a recent study by Aron, Monsell, Sahakian, and Robbins (2004) indicates a right prefrontal inhibitory function targeting task sets. Akin to the present study, they examined switching between stimulus attributes (words vs. arrows), with participants required to make a two-choice (left/right) discrimination on the basis of the value of the task-relevant dimension. Right frontal patients exhibited reliable RT and error switch costs compared to control subjects, in particular, when the values of the newly relevant and the irrelevant stimuli were bivalent. The authors proposed that inhibition of the former set was reduced in the right frontal patients, leading to an increase in errors when the response assignment of the now irrelevant stimulus conflicts with the response assignment of the newly relevant stimulus.

Although the findings by Aron, Monsell, et al. (2004) are consistent with the hypothesis that task-set inhibition has a right prefrontal basis, alternative interpretations are possible. Insufficient activation of relevant rules could easily increase susceptibility to interference from the irrelevant task dimension (e.g., Cohen & Dehaene, 1998), a problem that would show, in particular, on trials with bivalent, response-incongruent stimuli. Thus, evidence with an unambiguous indicator of task-set inhibition would be useful. Backward inhibition can serve this role because it cannot be explained in terms of insufficient task-set activation. Thus, our third goal was to reexamine the hypothesis of a right frontal inhibition deficit. If this hypothesis is correct, we should see reduced backward inhibition in right frontal patients compared to controls.

RESULTS

Figure 2 (top) shows RTs on no-switch and switch trials for univalent and bivalent conditions with single-task RTs included as baseline. We examined global and local switch costs both in absolute terms and relative to the single-task baseline to account for unspecific slowing in the patients. Compared to control subjects, patients with left frontal lesions exhibited increased global costs as reflected in RTs for univalent no-switch trials versus bivalent no-switch trials [absolute: $F(1,21) = 7.89$, $p < .02$; relative: $F(1,21) = 4.84$, $p < .04$]. Left frontal patients also exhibited larger local switch costs than control subjects across both univalent and bivalent stimulus conditions [absolute: $F(1,21) = 9.83$, $p < .01$; relative:

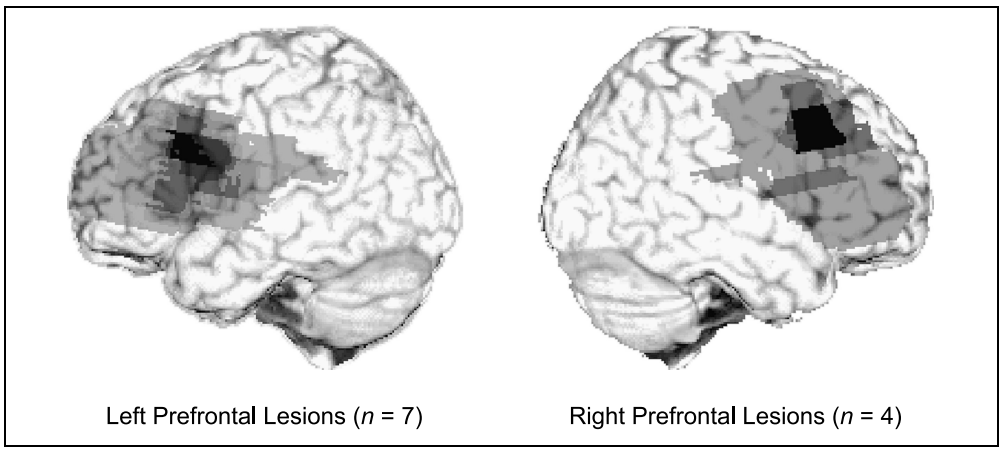

Figure 2. Extent of lesions for left and right prefrontal cortex patients presented as an overlay on a standard brain.

$F(1,21) = 7.41$, $p < .02$], and even when the univalent stimulus condition was analyzed alone [absolute: $F(1,21) = 9.74$, $p < .01$; relative: $F(1,21) = 8.61$, $p < .01$]. When comparing right frontal patients to controls, none of these effects were significant, all ps $> .3$.

The backward-inhibition effect reflects the tendency for people to need more time to return to a recently abandoned task set compared to a control situation in which a less-recently abandoned task set needs to be selected. In an analysis including controls and left frontal patients, the backward-inhibition effect was highly reliable [$F(1,21) = 8.14$, $p = .01$] (15 out of 16 controls and 6 out of 7 left frontal patients showed a backward-inhibition effect), and there was no reliable difference between groups [$F(1,21) = 1.21$, $p > .25$] (see Figure 3, bottom). If anything, left frontal patients showed numerically larger inhibition scores than controls. In contrast, right frontal patients exhibited a small backward-inhibition gain (two patients showed gains that were larger than the small costs showed by the remaining two patients). The difference between right frontal patients and controls was reliable [$F(1,18) = 5.89$, $p < .03$].[1]

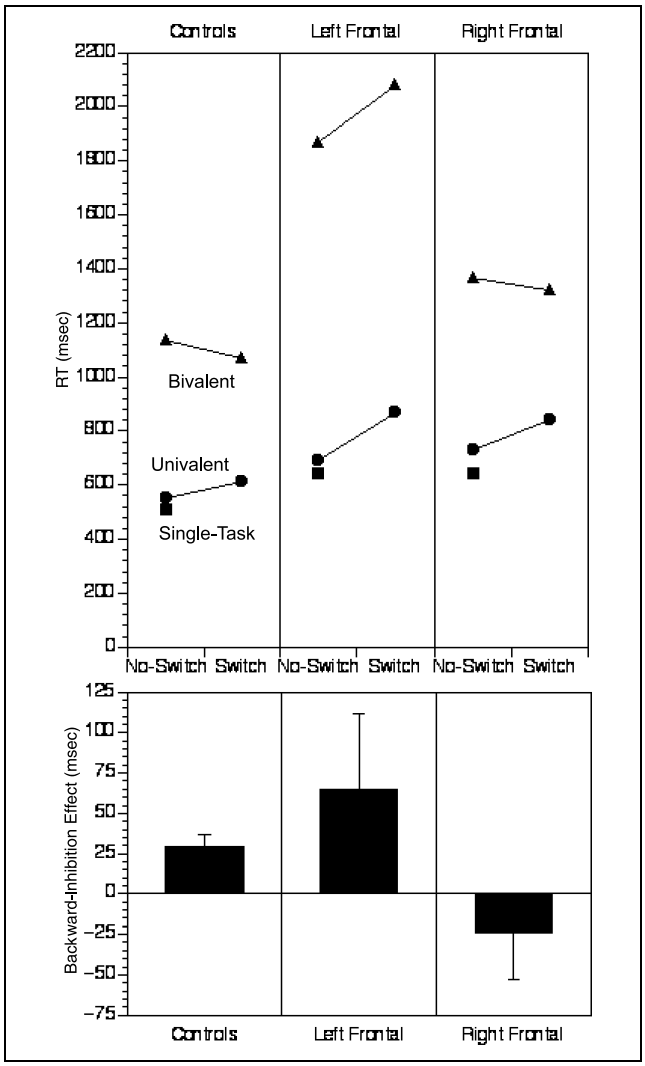

Figure 3. Top: RTs in the bivalent and univalent conditions for no-switch and switch trials as well as the single-task condition. Bottom: Backward-inhibition effect, measured as the difference in RT on trial n as a function of whether the $n - 2$ trial had been the same task set or a different task set. Positive scores indicate that the task set on trial $n - 2$ had been inhibited. Error bars reflect one standard error.

DISCUSSION

We replicated earlier reports of a left frontal set-selection deficit. This deficit appeared both in global switch cost, that is, the RT difference between bivalent and univalent no-switch trials, and as an additional cost at points where the response-relevant dimension changed. Interestingly, left frontal patients showed increased local switch costs even for univalent stimuli, that is, when no conflicting information was presented. This result is difficult to explain in terms of an inhibition deficit, but is compatible with a fundamental deficit in activating currently relevant task rules. Regarding the left prefrontal patients' increased global costs, Mayr and Kliegl (2003) (see also Altmann, 2004) have argued that in task-switching paradigms with trial-to-trial cueing of tasks, subjects undertake a cue-triggered retrieval process on every trial, even on no-switch trials. By this view, left frontal patients' increased global costs reflect a deficit in terms of activating/retrieving the currently relevant task set.

One aspect of our results requires further consideration. Neither controls nor patients with right frontal lesions exhibited local reaction-time switch costs in the bivalent condition. As indicated in the Introduction, this result is not all that surprising given that we had used a paradigm with a 75% switch probability. Such a situation may induce a bias towards treating every trial like a switch trial. Based on this interpretation, it seems possible that the local switch costs observed in left frontal patients reflect an inability adapting to switch probabilities rather than a switching deficit per se. However, a left frontal switch deficit was found even for the univalent condition where controls did show a reliable switch cost ($t = 7.56$, $p < .01$) and where strategic adjustments seem less probable. More importantly, a tendency for left frontal patients to be less prepared for set changes would actually counteract group differences in global costs (which are computed only on the basis of no-switch trials) and which did show a marked deficit in left frontal patients. In sum, we suggest that although we cannot rule out that differences in adjusting to switch probabilities may have played some role in local switch costs, the increased global costs observed in the left frontal patients reflect difficulties with cue-based selection of relevant task rules.

Is the set-selection deficit in the left frontal group associated with an inability to successfully inhibit irrelevant task sets? If activation of relevant rules and deactivation of formerly relevant rules are simply two sides of the same (prefrontal) function, then co-occurrence

of selection and inhibition deficits should be observed. However, there was no evidence for a left frontal involvement in task-set inhibition. If anything, left frontal patients showed (numerically) increased backward inhibition.

In contrast, patients with right frontal lesions did show a reduced backward-inhibition effect. Thus, the results provide a double dissociation with left frontal patients showing impairment in set activation/retrieval and right frontal patients showing impairment in task-set inhibition. The simplest interpretation is that there is a left frontal basis for activation/retrieval of task set and a right frontal basis for inhibition. Neuroimaging results have repeatedly demonstrated right prefrontal activations in situations that required resolution of response conflict or withholding a planned response, suggestive of an inhibitory function (e.g., Hazeltine et al., 2000; Garavan et al., 1999; Konishi et al., 1999). Moreover, our results are consistent with Aron, Monsell, et al. (2004), who reported greater task-set interference in right prefrontal patients after a task switch.

There is, however, one aspect in our results that does not match with the finding of Aron, Monsell, et al. (2004). Whereas those authors observed a switching deficit in right frontal patients, the right frontal patients in the current study performed more or less like normal controls (aside from the absence of the backward-inhibition effect). A procedural difference may have been responsible for this difference in results. In contrast to the random, trial-by-trial cueing of tasks in our study, Aron et al. used a so-called alternate-runs procedure in which switches between two different tasks occurred every three trials. It is likely that when subjects know that a task will stay the same for three trials, they will endorse it much more fully than when changes occur on a trial-by-trial basis. In turn, to disengage from a fully endorsed task set at the point of a task switch may require more inhibition. Thus, the situation used by Aron et al. may have been better suited to reveal the effects of an inhibitory deficit on switch costs than our study that required the random cueing procedure in order to establish the backward-inhibition effect.

In a follow-up experiment, we had tested all of the patients and a subset of 12 of the full sample of control subjects in a situation in which the response-relevant dimension was repeated for runs of three trials after which the cued dimension either switched to one of the three other possible tasks (75%) or remained the same (25%). Subjects performed six blocks of 60 trials in this experiment (following three practice blocks). Consistent with the results from the main experiment reported here, left frontal patients showed reliably increased RTs on no-switch trials (run position 1 vs. positions 2 and 3) and also increased switch costs (position 1 switch vs. position 1 no switch) compared to controls.

Interestingly, right frontal patients showed no generally elevated RTs on position 1 no-switch trials, but there was a trend in the direction of a switching deficit (180 msec for right frontal patients compared to 7 msec for controls). Although the difference between the two groups only approached significance [$F(1,14) = 3.01$, $p = .1$], it is consistent with the results reported by Aron et al. and with the idea that switch costs as a result of an inhibition deficit become apparent when longer runs of no-switch trials prompt full task-set endorsement. We therefore suggest that the backward-inhibition deficit is a more subtle indicator of an inhibitory problem that becomes manifest as a switch cost only in situations with high demands on task-set inhibition.

To summarize, the present findings indicate that task-set activation/retrieval is associated with the left prefrontal cortex, a result consistent with evidence from various other neuropsychological and neuroimaging studies (e.g., Aron, Monsell, et al., 2004; Brass & von Cramon, 2002; Rogers et al., 1998). Further, our results strengthen the case for a right prefrontal cortex involvement in task-set inhibition (see also, Aron, Monsell, et al., 2004). Taken together, these results suggest that the activation/retrieval of a relevant task set and the suppression of irrelevant task sets are functionally dissociable prefrontal functions.

METHODS

Participants

Seven patients with left prefrontal damage, 4 patients with right prefrontal damage, and 16 age-matched control subjects participated in the experiment. Patients were identified based on radiological review indicating a single, neurological insult restricted to the lateral aspect of the frontal lobe that had occurred at least 6 months before testing (Figure 2).

Lesion sizes and other characteristics for left and right hemisphere patients are shown in Table 1.

Apparatus and Stimuli

Stimuli were presented on a 16-in. Apple monitor positioned approximately 50 cm in front of the participants within a stimulus frame in form of a square with a side length of 5 cm. Verbal cues (''Word,'' ''Arrow,'' ''Circle,'' and ''Movement'') were presented near the top of the frame and indicated the relevant task dimension for that trial. For each cue, there were two stimulus values: For the cue ''Word,'' the response was based on whether a centrally presented word was ''left'' or ''right.'' For the cue ''Arrow,'' the response was based on whether an arrow, presented 15 mm to one side of fixation, pointed to the left or to the right. For the cue ''Circle,'' the response was based on whether a 5-mm-diameter circle was presented 35 mm to the left or to the right of

Table 1. General Information, Neuropsychological Assessment, and Lesion Information on the Subjects of the Control, Left Prefrontal, and Right Prefrontal Group

				WAIS-R										
	Age	*YOE*	*Sex*	*DS*	*PC*	*PA*	*BD*	*OA*	*DSS*	*BNT*	*COWA*	*TMT-A*	*TMT-B*	*Etiology*	*Volume (cm^3)*
Normal Controls															
AA	72	12	m						11	−2.2	1.1	−1.2	−0.4		
JB	64	12	m	12	12	18	16	18	16	0.1	−0.1	1.3	0.0		
JLB	64	12	f	10	15	12	16	13	8	1.3	−1.0	0.4	0.1		
FB	71	18	m						13	0.7	0.3				
BC	68	12	m												
MD	77	14	f	10						0.2	0.0				
GJ	74	14	m	18	17	16	16	15	18	1.0	3.0	0.5	0.9		
RJ	63	16	m		14	13	10	10	10	1.3	−0.2	0.1	0.8		
RK	74	14	f	15	13	13	10	15	16	0.7	−1.1	0.8	1.4		
NL	77	16	f	15						0.7	−0.7	−0.4	0.2		
JM	76	7	f	11	17	13	8	13	13	0.8	−0.6	0.2	0.5		
NS	79	18	f						14	0.8	0.0	1.0	0.8		
	71.6	13.8		13.0	14.7	14.2	12.7	14.0	13.2	0.5	0.1	0.3	0.5		
Left Prefrontal															
WA	77	14	f	7	15	15	12	15	9	−0.7	−2.5	−0.4	−0.3	Stroke	15.5
RC	52	12	m	7	11	12	13	11	8	−4.1	−2.5	−0.8	0.1	Arteriovenous malformation	56.9
EE	69	14	m	8	12	11	9	8	7	−2.2	−3.6	−1.4	−8.4	Stroke	40.9
MF	66	12	m	7	10	7	10	12	9	−0.2	−3.2	−0.9	−0.9	Stroke	34.4
DG	57	12	m	9	8		10					−0.1	−4.3	Meningitis	64.3
NT	59	15.5	f											Stroke	11.6
	63.3	13.3		7.6	11.2	11.3	10.8	11.5	8.3	−1.8	−3.0	−0.7	−2.8		37.3
Right Prefrontal															
EB	82	12	f	13	14	9	12	11	15	0.0	−0.6	1.3	0.9	Stroke	16.3
SR	9	12	f	10	9	11	10	5	8	−0.5	−2.0	1.0	−0.5	Stroke	10.4
BT	55	18	m							1.3	−0.8	1.3	0.4	Cyst	19.6
AP	73	12	f	13	10	9	9	8	11	1.8	1.0	−0.3	0.9	Stroke	135.4
	72.3	13.5		12.0	11.0	9.7	10.3	8.0	11.3	0.6	−0.6	0.8	0.4		45.4

Scores on the WAIS-R subtests are age-corrected seated scores with mean 10 and SD of 3. Lesion volume in cm^3 was measured after standardizing the brains to the MNI-template. YOE = years of education; DS = digit span; PC = picture completion; PA = picture assembly; BD = block design; OA = object assembly; DSS = digit symbol substitution; BNT = Boston naming test; COWA = controlled word association; TMT = trail making test.

fixation. For the cue ''Movement,'' the response was based on whether a series of dashes, presented 10 mm below and above fixation, were moving to the left or right (constant velocity of 5 cm/sec). Note that the ''Circle'' cue indicated the relevant stimulus, but that the actual response was based on the spatial location of the circle. Responses were made with the index and ring fingers of the preferred hand on two adjacent keys on the keyboard, indicating the spatial aspect (left or right) of the relevant task dimension.

Procedure

Each trial began with the appearance of the verbal cue. Two hundred milliseconds later, the stimulus displayed appeared (see below) and the cue and the stimulus remained present until a response was entered. Following a 100-msec pause, a new verbal cue appeared, signaling the start of the next trial.

All participants went through the same sequence of three experimental conditions. In the single-task condition, the relevant task dimension was held constant for all 50 trials of the block. There were four of these blocks, with all participants completing the blocks in the same order: word, arrow, movement, and circle. The verbal cue was presented on all trials, but did not change across trials within a block. The target was one of the two values of the cued task dimension. For example, if the cue was ''Circle,'' the stimulus display only contained the cue and a circle, either to the left or to the right of fixation.

The same displays were used in the univalent switching condition. Here, the relevant task dimension was randomly selected on a trial-by-trial basis (i.e., switch probability was 75%). Three 60-trial blocks of this condition were presented.

In the bivalent condition, two stimulus dimensions were present on each trial, one from the relevant set and one from an irrelevant set. For example, if the relevant dimension was ''Circle'' and the irrelevant (uncued) dimension was movement, the display would contain the verbal cue, a circle, either to the left or to the right of fixation, and the lines, moving either to the left or to the right. The irrelevant stimulus dimension changed every trial, even when the relevant dimension remained the same (i.e., on no-switch transitions). Each participant completed nine 60-trial blocks of the bivalent condition. The first three of these blocks were considered practice.

Data Treatment

RTs larger than 3 standard deviations from the mean, calculated separately for each participant, were excluded on a condition-by-condition basis. We also excluded error trials and trials following errors. Even in the bivalent condition, accuracy was high (controls: 4.8%, left frontal: 6.1%, right frontal: 4.4%) and in no case counteracted RT results. Therefore, we report RT results only.

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Note

1. We had planned to look at two additional indicators of set-level inhibition: negative priming (i.e., trial $n - 1$ irrelevant dimension becomes trial n relevant dimension) and ''inhibition gain'' (trial $n - 1$ relevant dimension becomes trial n irrelevant dimension), compared to a control condition (trial $n - 1$ relevant and irrelevant dimension different from trial n relevant and irrelevant dimension). None of the individual scores differed reliably from zero, therefore, we focused on the backward-inhibition score here. However, the pattern of numerical effects was consistent with the backward-inhibition results: For the negative priming measure, controls and left frontal patients showed costs (12 and 24 msec), whereas right frontal patients showed a benefit (103 msec); For the inhibition gain transitions, controls and left frontal patients showed benefits (14 and 63 msec), whereas right frontal patients exhibited no effect (−1 msec). Thus, on both of these measures, controls and left frontal patients tended to show numerical inhibition effects, whereas for right frontal patients inhibitory effects were eliminated or reversed.

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