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Dissociation of attentional processes in patients with focal frontal and posterior lesions

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Abstract

A location-based ('select-what, respond-where') priming task was used to examine three measures of selective attention (interference (INT), negative priming (NP), and inhibition of return (IOR)) as a function of focal brain pathology and the complexity of target selection. Control subjects showed different patterns of performance for the three attentional measures as a function of complexity, suggesting some independence among INT, NP, and IOR. Brain-damaged subjects showed significant response slowing, as well as a number of lesion-specific attentional abnormalities. Right frontal (including bifrontal) damage resulted in proportionally increased interference related to task complexity. Left posterior damage increased IOR in the most complex task, while left frontal damage reversed the control pattern of IOR as a function of complexity. Right hemisphere (right posterior and right frontal damage) pathology resulted in a virtual loss of negative priming at all levels of task complexity; left and bifrontal damage resulted in diminished NP only related to increases in the complexity of selection. INT, NP, and IOR are mediated by different brain regions and their expression can be modulated by the complexity of the selection task. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Attention; Interference; Inhibition of return; Negative priming; Task complexity

1. Introduction

Frontal lobe damage often results in distractibility, neglect, perseverative behaviour, and impulsivity [6,14,35]. From these clinical observations and from an analysis of frontal lobe projections, a number of cognitive theories have been developed that give an account of the highest levels of attentional control by frontal lobe structures. Shallice [31,44] proposed a detailed model of a frontally-based supervisory system that controls the development of attention in non-routine situations. Posner [39] differentiated an anterior attentional system from a sensory-driven posterior attentional system. The former controls stimulus selection and the allocation of mental resources; the latter is modulated by the anterior system and controls lower-level aspects of attention (e.g., disengagement from a currently selected location). Mesulam [24] proposed a model in which attentional functions are also widely distributed throughout the brain but emphasized several central roles played by anterior structures in the control and direction of attention. Shimamura [48], following the path of several early theorists, emphasized an inhibitory attentional role of the frontal lobes in controlling complex behaviours.

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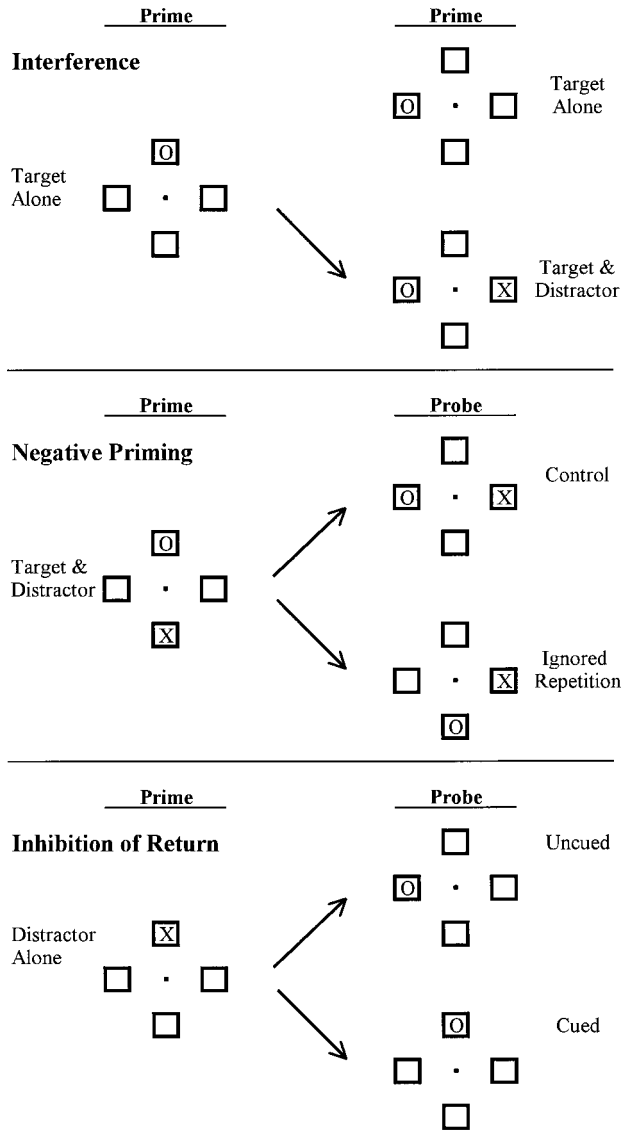


Fig. 1. Examples of the measurements obtained by comparison of various displays for the OX task. See text and Methods for exact details of stimuli presentation. Subjects viewed a computer screen on which four potential target locations were indicated by boxes, and were required to indicate the location of the target with a joystick. 'O' was the target and 'X' the distractor. Each trial consisted of a prime and a probe display. Display trials were of three types: Target alone, target-plus-distractor, or distractor alone (no-go trials). Interference (INT) was measured as the difference between target alone and target-plus-distractor prime displays. The two probe displays following prime display in the INT condition were not analysed. Negative priming (NP) was measured as the difference between control and ignored-repetition probe displays. Inhibition of return (IOR) was measured as the RT difference between cued and uncued probe displays. The no-go trials were not analysed.

Despite this extensive theorizing, the experimental studies investigating the nature of attentional deficits following frontal lobe damage have been relatively few, and the results sometimes inconsistent (for reviews, see [52,53,55]). For example, Stuss et al. [54] found that patients with large frontal lesions following prefrontal leucotomy performed as well as, or even better than, matched control subjects on several measures of attention including the Stroop test. More recent studies have investigated patients with more circumscribed lesions, but the results of those studies are not entirely consistent. Thus, while right frontal damage has been strongly associated with deficits in sustained attention [13,65,67], damage to this region has also been shown to disrupt selective attention [2,19,20] as well as attention to extrapersonal space [5,15,49]. Similarly, vulnerability to interference has been related to both orbital frontal regions [12,34,38,56] and dorsolateral frontal cortex [27].

There are many reasons for the relative dearth of studies and for the lack of consistency and specificity in the results. These include difficulties in finding suitable patients with focal lesions, the lack of precise information on lesion location, and the different ways in which attentional processes have been tested and measured. There is reasonable evidence to indicate that fractionation of possible anterior attentional processes is the appropriate approach [3,44,53,57]. To examine further this potential fractionation of frontal lobe processes, we assessed theoretically defined measures of attention in patients with well documented lesions.

We employed a spatial-selection paradigm, shown graphically in Fig. 1. There were two displays for each trial, the first called a 'prime' and the second a 'probe'. In each display, a target alone, a distractor alone, or both together were presented. The content of the target and distractor, and the location of each, varied as described below.

Subjects were required to identify a target on the computer monitor and move a joystick to indicate its location. The structure of the task allowed us to assess three potentially dissociable measures of attention: interference, negative priming, and inhibition of return [48,59,60]. Interference (INT) is measured as the difference in reaction time to select a target presented in isolation (in one prime display), compared to when that target is presented simultaneously with a distractor (in a prime display in a different trial. In these instances, the probe RT is not used). Both negative priming (NP) and inhibition of return (IOR) (or response inhibition) are measured as an increase in response latency to select from the probe display a target location previously occupied by a distractor in the prime display. NP and IOR differ in the nature of the attentional response on the prior or 'prime' display. For NP, a target appears (in addition to the distractor) and is successfully selected in the prime display. For IOR, in contrast, only a distractor appears in the prime display and thus no overt selection response is made (i.e., a no-go trial). In other words, INT measures the effect of a distractor on target selection; NP measures a

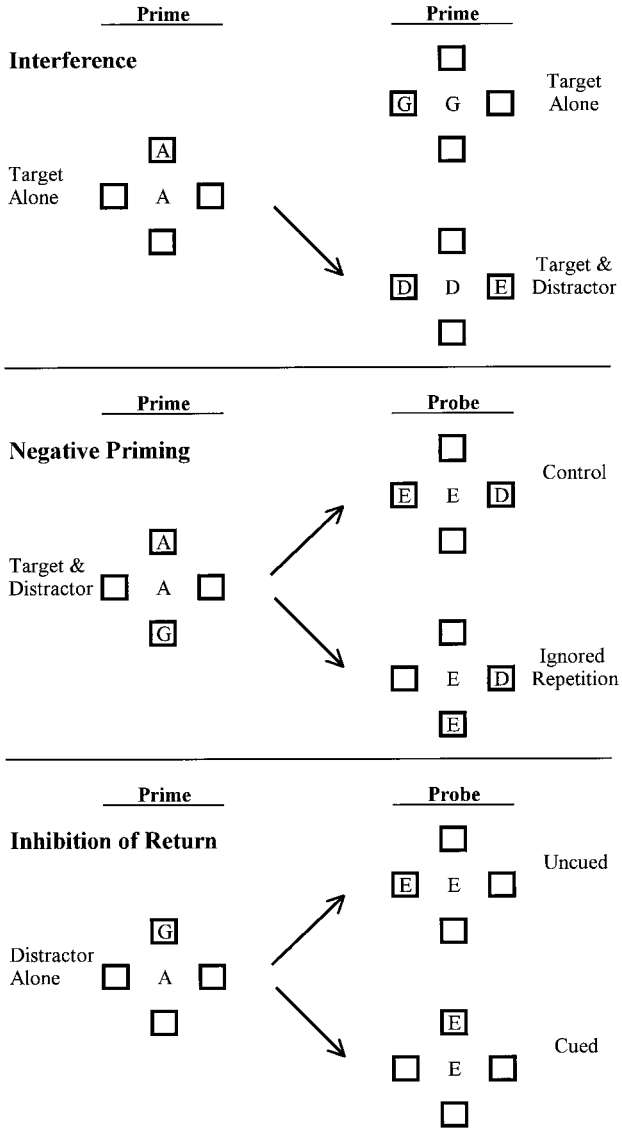


Fig. 2. Examples of the prime and probe displays for the UU task. Description of this task and its associated attentional measures is the same as that for the OX task (see legend for Fig. 1) with the exception that the target was indicated by a centrally presented cue.

change in selecting a target location, when that location was previously occupied by a distractor in a previous target-present trial; IOR measures the effect of selecting a target location when, on a previous trial, that same location response had to be suppressed (or was otherwise contra-indicated).

This task has been described as a 'select-what, respond where' task because, although subjects are required to make a spatial location response, target selection occurs on the basis of stimulus identity. Most previous studies using this task [60] have employed a single target that remains constant throughout testing (e.g., the letter 'O'), thus making selection relatively well defined. However, a central finding in research with frontal lobe patients is that deficits may be observed only under conditions of uncertainty or high task demands [53]. We therefore developed three versions of the tasks that varied the complexity of selection.

In the basic 'OX' task (Fig. 1), investigated previously in normal subjects [61], only the symbols 'O' and 'X' were used, with O always being the target and X always being the distractor. Thus target and distractor were distinguishable at the level of simple features and were consistently mapped throughout the testing [46]. In the second (Upper case–Upper case: UU) task, four different letters were used, all presented in upper case. The target, one of the four letters, changed from display to display. The target was defined for each display by presenting one of the four letters in the center of the display (Fig. 2). When distractors were present, they were one of the three other letters. Thus, subjects had to identify the current target in the center, locate its match (either by physical shape or letter identity) in one of the four target locations, and make a spatially defined response as quickly as possible. In the third, most demanding, task the same four letters were used but the central cue was now presented in lower case, whereas the target and distractors were in the upper case (Lower case–Upper case: LU task). The letters used were perceptually different in their lower and upper cases (e.g., e/E), and thus a more complex matching process was required for correct identification of the target [37]. The rationale underlying this task manipulation was to examine if lesions in different brain regions affected sensitivity to stimulus complexity. Being consistently mapped, the less demanding OX task may be performed more automatically and thus may not necessitate involvement of the frontal lobes, whereas tasks requiring more elaborate analysis, in particular the LU tasks, may necessitate frontal lobe involvement. Tasks also may differ in their demands on the left and right hemispheres, depending on the content of identification or type of attentional demand. For example, perceptual matching may relate primarily to the right hemisphere.

In the results that follow, we first report general reaction time (RT) effects for all groups. We examine the entire pattern of performance for the control group as a function of the complexity of selection (OX, UU, and LU). These patterns were then used as a template with which to compare the performance of patient groups.

2. Methods

2.1. Subjects

Six groups of subjects were tested. Five of the groups consisted of patients with lesions confined to

Table 1
Demographic descriptions of the control and patient groups

	Gender		Age (years)		Education (years)		Hand	
Group	Male	Female	*M*	SD	*M*	SD	Right	Left
Control	8	11	49.47	16.26	14.21	2.32	18	1
Left frontal	4	2	54.33	10.13	14.33	3.88	6	0
Right frontal	6	4	49.70	16.34	12.30	2.67	10	0
Bifrontal	2	4	49.33	12.99	10.67	2.50	6	0
Left posterior	1	6	50.43	17.46	13.00	1.29	7	0
Right posterior	5	2	51.10	15.60	13.40	2.90	5	1

the frontal or non-frontal regions. The three frontal groups were patients with lesions restricted to the right frontal, left frontal, or bifrontal regions. The two posterior groups had lesions restricted to the left or right non-frontal regions. The demographic data of these groups are summarized in Table 1. The lesion location and etiology data are summarized in Table 2. The lesion locations for each subject in each group are depicted in Fig. 3A-E. The examination of lesion-behaviour relationships after frontal injury is complicated [57]. Etiology may be one factor affecting results. However, without including patients with different etiologies, the ability to obtain patients with single localized lesions confined to the frontal lobes or immediate frontal systems is highly limited. To control for the effect of different etiologies, we tried to confine the tumor patients to those with focal encapsulated tumors that had been successfully removed, and to ensure that any traumatic brain injured patients had primary focal contusions, with likely less diffuse axonal injury. Lesion volume was quantified using a pixel tabulation method. For each patient, for each axial slice in which a lesion was evident, the size of the lesion was quantified by superimposing the lesion on a constant pixel diagram and counting the number of pixels. This provided a method of comparing lesion size across groups. Although all scans were available for localization, several scans were missing for quantification: LF = 2; RF = 1; BF = 1; LNF = 2; RNF = 2.

Table 2
Lesion location and etiology within patient groups

Subject no.	Etiology	Lesion location
Left frontal lobe		
2023	Stroke	Dorsolateral, Occipital
2056	Tumor	Dorsolateral
2029	Stroke	Striatal
2012	Tumor	Striatal, Superior Medial
2100	Stroke	Medial, Septal
2111	Stroke	Dorsolateral
Right frontal lobe		
2001	Stroke	Dorsolateral, Striatal
2018	Stroke	Dorsolateral, Striatal
2024	Stroke	Dorsolateral, Striatal
2027	Stroke	Dorsolateral, Striatal
2006	Stroke	Striatal, Inferior Medial, Septal
2005	Tumor	Medial, Dorsolateral
2019	Trauma	Medial, Dorsolateral, Temporal
2011	Stroke	Superior Medial
2047	Stroke	Inferior Medial
2107	Lobectomy	Dorsolateral
Bilateral frontal lobe		
2002	Infarct	Medial, Dorsolateral
2045	Stroke	Medial, Septal
2013	Stroke	Inferior Medial, Septal
2014	Stroke	Inferior Medial
2042	Trauma	Inferior Medial
2104	Lobectomy	Inferior Medial, Dorsolateral
Left Non-frontal Regions		
2010	Stroke	Parietal
2016	Stroke	Parietal
2031	Stroke	Parietal
2028	Stroke	Temporal, Occipital
2032	Lobectomy	Temporal
2036	Lobectomy	Temporal
2038	Lobectomy	Temporal
Right Non-frontal Regions		
2008	Tumor	Temporal, Parietal
2021	Stroke	Temporal, Occipital
2040	Lobectomy	Temporal
2055	Hemorrhage	Temporal
2108	Stroke	Temporal
2025	Stroke	Parietal
2043	Stroke	Occipital

The control group consisted of 19 individuals with no history of neurological or psychiatric sequellae, matched as closely as possible to the patient group. To ensure that a basic level of performance was present to complete the tasks, various neuropsychological tests were administered (Table 3). All groups had levels of IQ functioning and digit span forward within the normal range. All subjects could understand the task demands. Subjects with clinically detectable neglect were excluded. There were no significant group differences in age and education.

2.2. Tasks and procedure

Three spatial selective attention tasks were used, each providing RT measures related to operational definitions of interference, negative priming, and re-

sponse inhibition (see below). Each task was similar in its demand. The subject had to identify and locate a defined target stimulus by moving a joystick in the same direction on the joystick as the stimulus on a computer monitor, while ignoring a possible concurrently presented irrelevant stimulus. They differed in the level of complexity and task demands, related to the identity of the target stimulus.

In the OX task, the target stimulus was defined as the letter O and the distractor, when present, was the symbol X. The two other tasks were letter matching paradigms, using the letters A, D, E, and G. The target varied across trials, and was identified by its simultaneous appearance in the center of the screen. If the target was A, then the distractor would be one of the remaining three letters. In one of the letter matching tasks, labeled as UU (upper–upper), all of the letters were printed in upper case. In comparison to the OX task, the UU task had the additional requirement of central letter identification (A, D, E, or G), and then matching perceptually the target stimulus in order to make an appropriate response. The second letter matching task was called LU (lower–upper) since the center letter was printed in lower case, while the target and distractor stimuli were presented in upper case. This task therefore had the additional demands of at least a literal identification (i.e., e–E) as opposed to a simpler perceptual match. The OX and UU tasks are schematically depicted in Figs. 1 and 2.

Each trial always consisted of two separate displays,

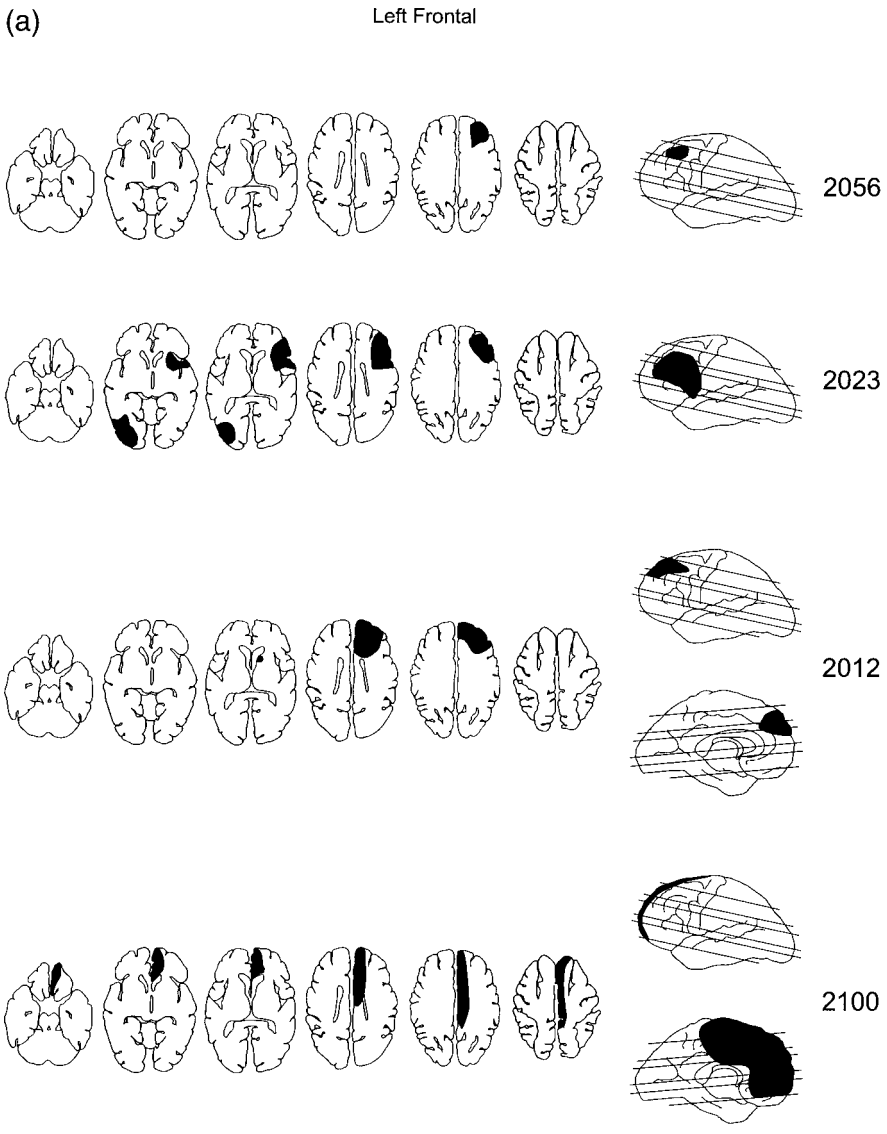


Fig. 3A-E. Schematics of lesion location. The lesion location for the available scans for each patient in each of the patient groups is illustrated. In some cases, lesion location had been documented, and the scan subsequently was lost. To assess frontal systems, and because of our prior research [51], we included in the frontal group patients with striatal lesions. 3A = LF; 3B = RF; 3C = BF; 3D = LP; 3E = RP.

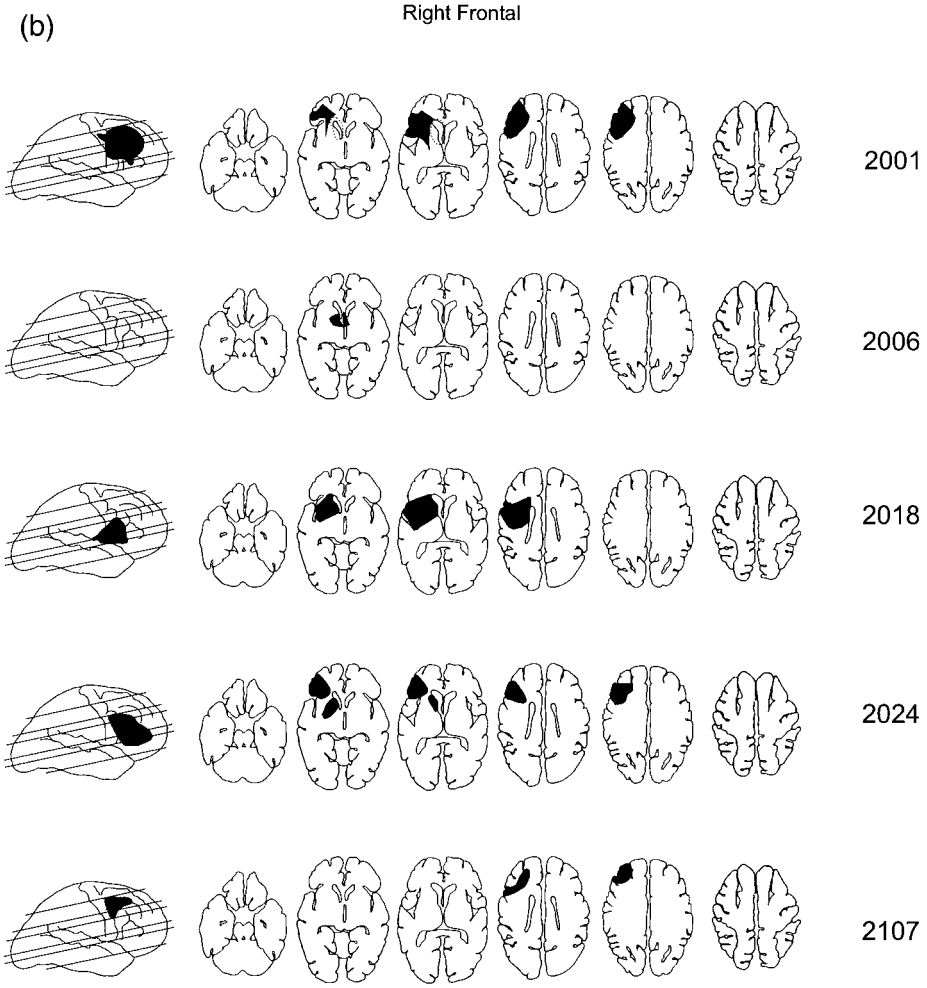


Fig. 3 (*continued*)

a PRIME and a PROBE. The prime display could be one of three types: target alone, target with distractor, or distractor alone. The interference measure was obtained solely by comparing prime displays, subtracting target alone from target/distractor displays. The greater the difference in RTs, the greater the interference, suggesting that the presence of an irrelevant distractor in the display slowed RT response to the target greater than if the target appeared alone.

Only two probe displays were relevant to the defined measures, and these followed the target/distractor and distractor alone displays. Target/distractor prime displays were followed by control or ignored repetition displays. In the control probe display, the target and distractor were located in positions not used in the prime display. In the ignored repetition probe display, the target was in the location previously occupied by the distractor in the prime display, and the probe distractor in one of the two positions unoccupied in the prime. Comparison of these two probe conditions that followed target/distractor primes provided the negative priming measure, defined by slower RTs in the ignored repetition compared to the control probes display. This would indicate that there was active suppression of the location previously occupied by the distractor.

Distractor alone primes were followed by non-cued (target was in one of the three locations not occupied during the preceding prime display) or cued (the probe target was in the location of the prime distractor) probes. Inhibition of return was defined by slower RTs in the cued compared to the non-cued probes, indicating that, even though a response had not been made in the distractor alone prime, the response inhibition continued into the probe display, slowing the response to the cued target.

Each trial was subject initiated with a button press on the joystick box. Timing of displays for each trial was as follows: trial initiation; 1500 ms delay; prime display and response; response stimulus interval of 357 ms; probe display and response. The prime and probe display duration, when a target was present, remained on the screen until a response was made or 3000 ms

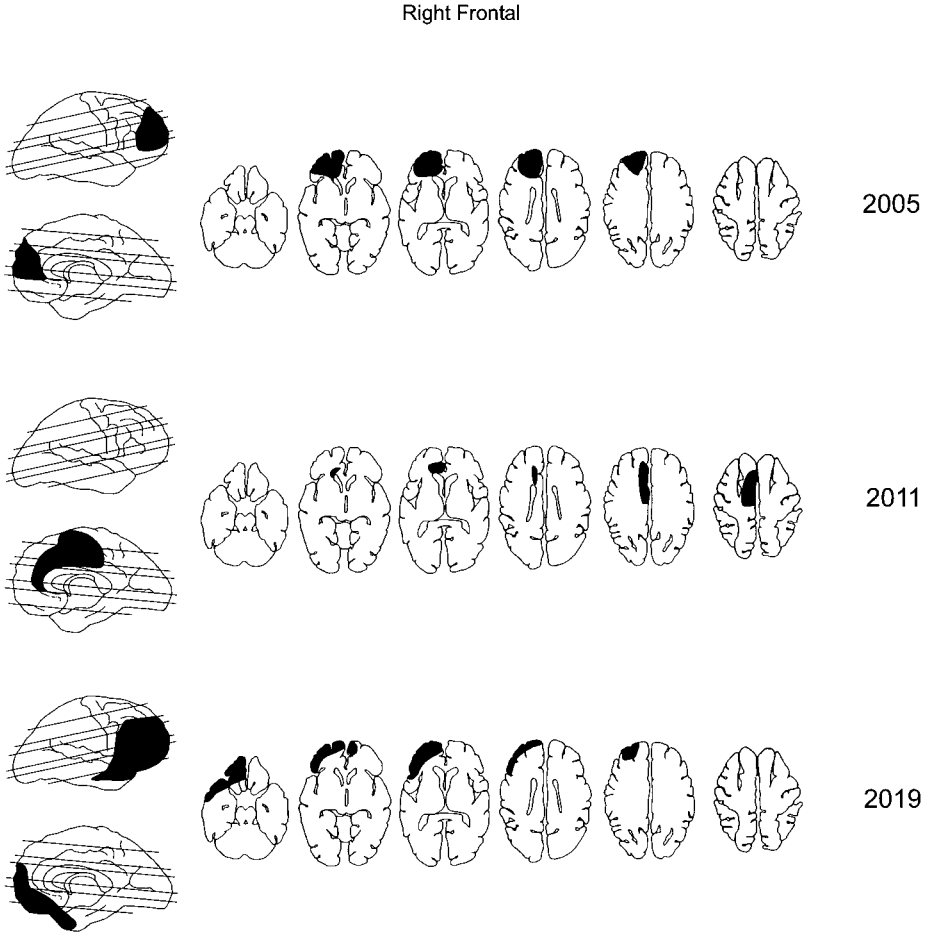
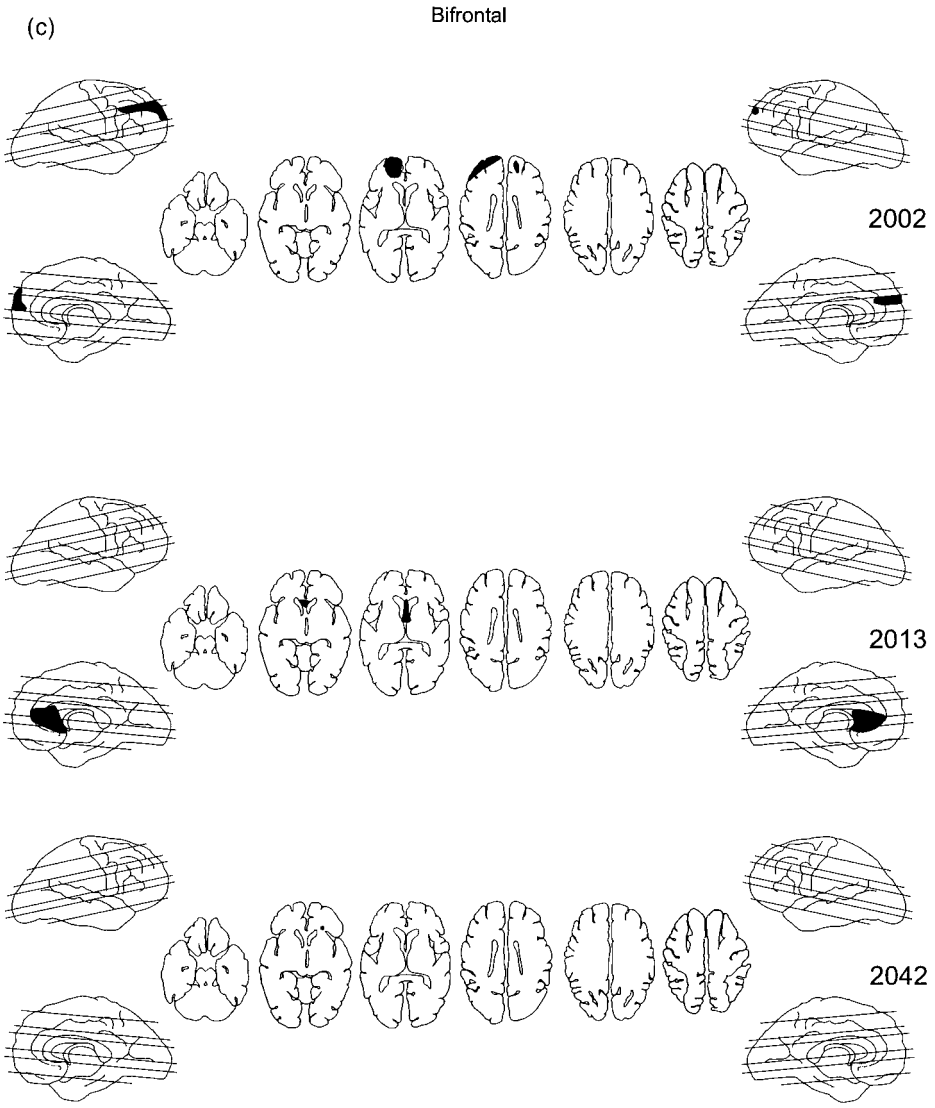


Fig. 3 (*continued*)

had elapsed. If a target was not present, the stimuli remained on the screen until the subject's mean RT for the particular display type (continuously updated after an initial set at 1000 ms) plus an additional 500 ms had elapsed [60]. Incorrect responses were indicated by a brief beep. A prompt to press the start key reappeared on the screen following probe response or the appropriate delay for no-go probes.

Blocks of 12 trials, each of six conditions appearing twice, were presented until the subject reached a defined number of correct responses for each of the six conditions. The criterion for the practice trials was four correct, and for test trials 20 correct per condition. The analyses were based on these correct responses. To investigate possible speed-accuracy tradeoff effects [8,29,32,45], group differences in errors for all tasks and conditions were analysed. The proportion of errors for each task and condition is summarized in Tables 4–6. The only group to make significantly more errors compared to any other group were the left posterior patients. This was observed only in two instances: OX target alone ($F(5,49)=4.0$, $P = < 0.01$) (left posterior > control, bifrontal and right posterior groups), and LU target alone ($F(5,49)=3.4$, $P = 0.01$) (left posterior > control group). None of the other analyses were significant. The mean number and range of test trials for each of the groups was as follows: LF = 23.1 (22–26); RF = 23.4 (20–32); BF = 22.5 (20–28); LP = 25.5 (22–40); RP = 22.5 (20–26); CTL = 21.4 (20–24). Since the left posterior group was the one that most resembled the control group in performance and this group was the only one to show significantly increased errors, the results are interpreted as being independent of speed-accuracy trade-off effects.

Approximate viewing distance was 60 cm. A 1 mm square fixation point subtending 0.1° of visual angle horizontal and vertical indicated the center of the computer monitor. Four 20 × 20 mm squares were presented above, below, left, and right of the center square, each square 25 mm from the fixation point. These four squares, subtending 1.1° horizontal and vertical, were the locations where the target and distractor stimuli could appear. The boxes and fixation point were light grey in colour. The stimuli were green. The joystick was affixed to the table surface, immedi-



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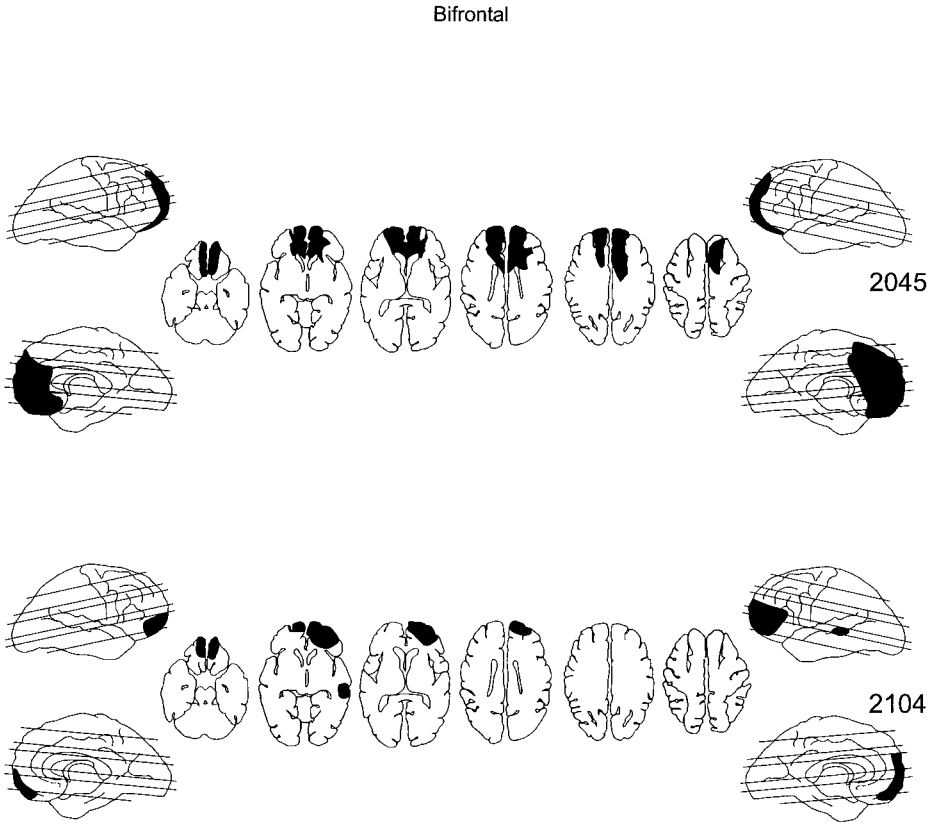
ately in front of the computer. Order of tasks were randomly administered to all subjects. For each task, the subject was instructed about the type (OX, UU, LU) and meaning (target, distractor) of the stimuli, and told to move the joystick in the direction consistent with the target location as quickly as possible while trying not to make mistakes.

3. Results

3.1. Analysis of baseline RTs

To assess the general effects of task complexity (OX, UU, and LU) and brain injury on RT, we first examined performance on the most simple selection trials, those in which a target was presented without distractors in one of the four possible locations (Target-Alone display). There was no significant group by task interaction ($F(10,98) = 0.53$, $P = 0.87$). Complexity of attentional selection had a significant effect on RT for all groups ($F(2,98) = 79.9$, $P < 0.001$) (Fig. 4). There was a significant main effect of group ($F(5,49) = 6.8$, $P < 0.001$]. The LF (slowest), LP, RF and BF groups were significantly slower than the CTL group. While the RT of the RP group was slowed in relation to control subjects, this did not reach significance.

The slowing exhibited by the patient groups complicates analysis of the more specific attentional measures. One major problem associated with slowing is that analyses of variance (ANOVAs) performed on difference scores (i.e., priming measures) will often show significant Group by Task interactions despite similar proportional increases in RTs from prime to



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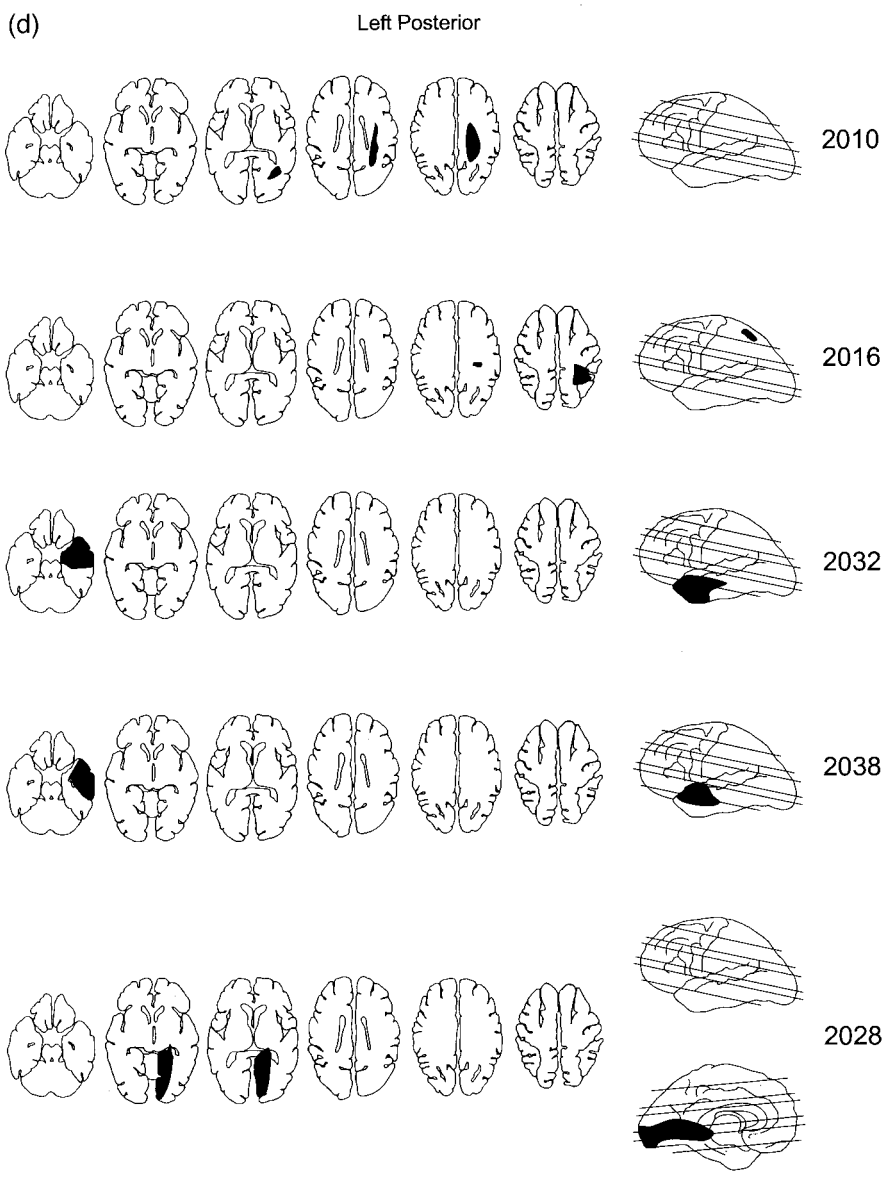
probe conditions. A similar problem arises when making comparisons within a group across tasks with different baseline RTs (such as occurs for the tasks of increasing complexity used here). Given our interest in selective processing deficits, we adopted the conservative assumption that task and group effects are only revealed by disproportionate effects on RT. That is, we computed the proportional increase in RT in the critical conditions relative to their appropriate baseline conditions: Interference (INT) = ((target + distractor) − (target alone))/(target alone); Negative Priming (NP) = ((ignored repetition) − (control trial))/(control trial); Inhibition-of-Return (IOR) = (cued–uncued)/(uncued).[2] In general, proportional scores showed effects that were qualitatively similar to those identified with absolute difference scores. All observed RTs are provided in Appendices A–C.

3.2. Analysis of control subjects

Fig. 5 shows the proportional scores for the different measures (INT, NP, IOR). For the interference measure there was a significant task effect ($F(2,36) = 29.4$, $P < 0.001$). OX produced less interference than the UU and LU tasks, which were not different from each other. Negative priming was evident for all three tasks; however, there were no significant differences among the three complexity levels. For inhibition of return, post hoc analysis[3] of the significant task effect ($F(2,36) = 5.5$, $P < 0.01$] revealed that OX produced more IOR than the other two tasks. Although the UU and LU tasks were not different

[2] The use of proportional (ratio) scoring is based on the assumption that all processes underlying task performance processes are slowed at the same rate ('general slowing'). If, in contrast, there is differential slowing of task-relevant processes (as might be the case with focal brain damage), proportional scoring would not provide a completely accurate depiction of performance. However, without a priori knowledge of the specific processes underlying task performance and their neurological basis, any of a number of corrections for slowing could be appropriate (see [4], for a discussion of similar issues in the context of age-related slowing). The alternative of examining only absolute difference scores seems equally, if not more, theoretically suspect, as slowing of any form will tend to magnify absolute differences between conditions. Thus, although proportional scoring may fail to capture the complexity of lesion effects on attentional processes (i.e., there may indeed be process-specific slowing), we view it as a better approximation to the 'true' state of affairs than absolute difference scores. More importantly, the central conclusions we wish to draw are based on patterns of performance that are qualitatively similar when calculated as absolute or proportional differences.

[3] Based on Tukey's HSD $P < 0.05$, as were all other post hoc comparisons.



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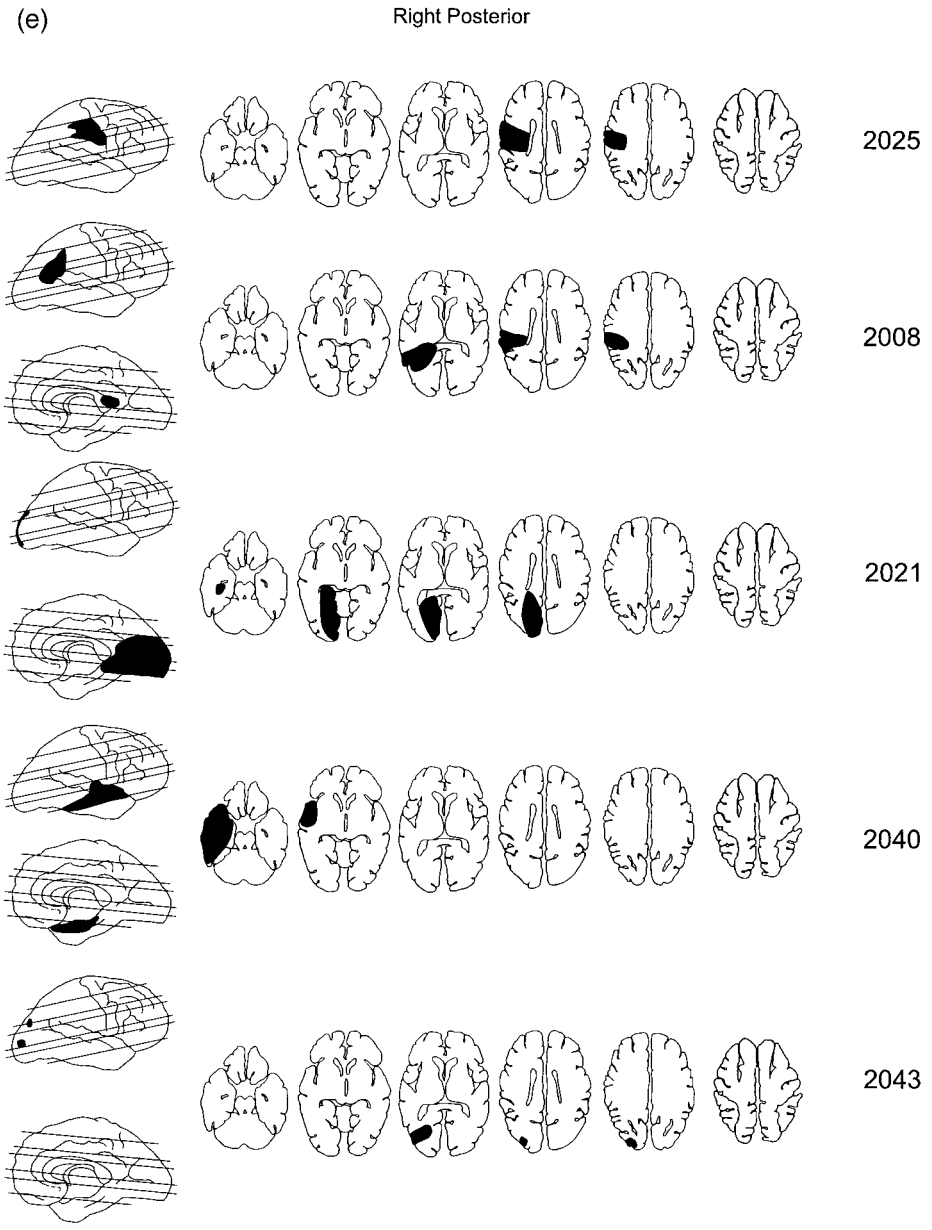
from each other, there was a trend to decreasing IOR with increasing task complexity. In summary, as the complexity of attentional selection increased across tasks, interference increased, IOR decreased, and NP showed no effect.

4. Discussion of control subjects

This study employed a location-based ('select-what, respond-where') task to examine three measures of selective attention—interference, negative priming, and inhibition of return. Critical to our design was a manipulation of the complexity of target selection. This manipulation allowed us to assess the generality of the three attentional measures. Moreover, if complexity of selection affects how the three measures of attention get expressed, it would have important implications for the interpretation of these measures in patients with focal brain pathology. In fact, the complexity of selection was found to have dramatic influence on the three measures of attention. These results support the claim that these measures are indexing different (and dissociable) underlying processes. We discuss the three patterns of performance in control subjects below.

4.1. Interference

INT reflects the increased difficulty of identifying and responding to target stimuli in the presence of non-target (distractor) stimuli, and is a basic measure of the efficiency of attentional selection. Interference



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was greater, both proportionally and in absolute terms, with increases in the complexity of target selection. Larger amounts of interference indicate an increased intrusiveness of the distracting stimuli, resulting in less efficient selection of, and/or responding to, the target items. A number of factors, either alone or in combination, seem relevant to explaining this increasing interference. One concerns the number of processing steps needed for target selection. In the OX task, only one comparison is needed in order for the target to be identified, that between O and X. In contrast, the UU and LU tasks potentially require two comparisons, one for each of the possible targets in relation to the cue. Moreover, the LU task requires a transformation of the cue and/or target. In this regard, it is noteworthy that three of the four letters employed (E, G, and D) were subject to phonemic/acoustic confusions. If comparisons in the LU task were being made on the basis of a phonemic code [38], such confusions could be expected to act as an additional source of interference in identifying and selecting the target.

While the LU task did increase the level of interference relative to the physical-matching UU task (a proportional increase of 0.04), the increase was considerably smaller than the increase observed from the OX to UU task (0.12). Doubling the steps required for both the UU and the LU tasks provided the maxi-

Table 3
Baseline tests of the control and patient groups

Group		NART[a]	BNT[b]	JOL[c]	Fluency		Digit span		
					Verbal-F	Semantic	Total	Fwd	Bwd
Control	*M*	113.79	55.63	27.05	12.84	22.57	14.95	8.47	6.47
	SD	5.97	3.73	3.61	3.30	8.28	3.31	1.74	1.84
Left frontal	*M*	104.79	48.75	21.83	7.80	12.80	8.67	5.67	3.00
	SD	6.87	10.94	5.19	3.35	2.39	1.37	0.52	1.10
Right frontal	*M*	104.79	52.30	23.89	10.60	13.80	11.10	6.20	4.90
	SD	9.10	5.68	4.37	2.12	3.46	3.00	1.48	1.73
Bifrontal	*M*	98.68	46.17	22.80	7.67	11.17	10.67	6.33	4.33
	SD	9.43	11.86	5.31	3.50	3.92	0.82	1.03	0.82
Left posterior	*M*	104.51	48.57	23.57	7.71	12.71	10.29	6.14	4.14
	SD	7.21	5.56	5.00	4.46	4.46	2.36	1.35	1.77
Right posterior	*M*	111.30	56.30	26.70	15.10	18.40	13.30	7.60	5.70
	SD	9.20	2.90	3.10	3.60	4.20	2.70	1.00	1.80

[a] NART = National Adult Reading Test IQ Estimate.
[b] BNT = Boston Naming Test, 60 item version.
[c] JOL = Judgement of Line Orientation.

Table 4
Proportion of errors for O–X task

		Target alone	Target and distractor	Control	Ignored repetition	Uncued	Cued
Control	*M*	0.59	0.80	1.67	0.93	1.85	1.39
	SD	1.26	2.01	3.10	1.85	3.61	2.10
Left frontal	*M*	1.08	1.73	1.45	4.42	3.52	5.42
	SD	1.78	2.05	2.25	4.85	3.15	7.66
Right frontal	*M*	3.48	2.33	3.37	4.30	2.09	5.57
	SD	2.71	2.71	4.31	4.01	2.95	5.61
Bifrontal	*M*	0.73	0.35	0.00	2.08	0.75	2.83
	SD	1.14	0.86	0.00	5.10	1.84	5.07
Left posterior	*M*	5.17	1.34	3.51	5.00	4.24	3.59
	SD	6.68	2.03	6.82	9.57	4.64	2.63
Right posterior	*M*	0.33	1.89	2.47	2.49	0.00	2.49
	SD	0.87	2.02	2.33	3.52	0.00	3.52

Table 5
Proportion of errors for U–U task

		Target alone	Target and distractor	Control	Ignored repetition	Uncued	Cued
Control	*M*	0.33	1.03	2.03	2.05	0.91	0.24
	SD	1.42	1.79	5.81	3.86	2.28	1.03
Left frontal	*M*	1.35	3.18	0.75	2.77	3.30	4.88
	SD	2.37	2.06	1.84	3.40	5.21	4.69
Right frontal	*M*	1.40	1.61	4.39	4.83	2.85	2.85
	SD	2.06	2.99	6.26	6.63	5.03	3.32
Bifrontal	*M*	0.73	1.38	2.88	0.70	2.78	1.38
	SD	1.14	3.39	3.45	1.71	6.82	3.39
Left posterior	*M*	4.83	3.10	6.01	5.77	3.04	5.07
	SD	7.87	5.71	7.51	5.95	4.09	11.67
Right posterior	*M*	0.64	0.90	1.93	0.64	0.00	1.29
	SD	1.70	2.38	2.41	1.70	0.00	2.20

Table 6
Proportion of errors for L–U task

		Target alone	Target and distractor	Control	Ignored repetition	Uncued	Cued
Control	*M*	0.11	0.81	1.52	3.16	0.24	0.46
	SD	0.48	1.29	2.79	3.72	1.03	1.37
Left frontal	*M*	0.98	4.42	3.30	6.78	2.78	0.63
	SD	1.62	3.53	5.21	5.23	2.17	1.55
Right frontal	*M*	3.27	6.67	4.33	3.62	5.11	3.69
	SD	3.94	8.10	3.87	5.94	7.29	7.96
Bifrontal	*M*	1.28	4.92	2.57	6.65	0.60	0.00
	SD	2.22	4.86	3.99	4.85	1.47	0.00
Left posterior	*M*	6.27	8.27	9.74	11.71	2.50	5.81
	SD	8.57	10.26	14.80	15.73	6.61	11.39
Right posterior	*M*	1.60	3.37	0.60	2.49	1.19	0.00
	SD	1.70	4.11	1.59	2.33	3.14	0.00

mum increase in interference. However, there was a second, possibly more basic, factor responsible for the increasing interference—degree of uncertainty as to target identity. That is, in contrast to the consistent mapping of target (O) and distractor (X) in the OX task, targets and distractors changed roles from trial to trial in the UU and LU tasks. It is possible that such variable mapping [46] produced a form of proactive interference that decreased subjects' efficiency in identifying and/or responding to the target, thus increasing the degree of interference. A related explanation appeals to the degree of controlled and automatic processing in the various tasks. That is, consistently-mapped tasks (such as the OX task) are known to facilitate use of automatic processes, whereas performance in variably-mapped tasks (UU and LU) requires continued attentional control. Note, however, that neither factor (proactive interference or the need for attentional control) appears to affect the levels of NP and IOR (i.e., neither measure increased from OX to UU). That different factors are relevant to the expression of the three measures supports the claim that they reflect dissociable processes.

Regardless of the specific explanation, the most important point to note is that the magnitude of interference is sensitive to changes in the basis of selection. This finding has implications for theoretical explanations of interference, as well as for identifying the neural systems involved (as we discuss later).

4.2. Negative priming

NP was initially thought to reflect an inhibitory process that operated during selection (on the prime trial) to reduce interference from available distractors, and thus enhance target selection [28,58]. However, this measure has also been characterized as reflecting a post-selection inhibitory process that prevents recently rejected information from gaining access to effectors [23]. One of the main sources of evidence for the latter

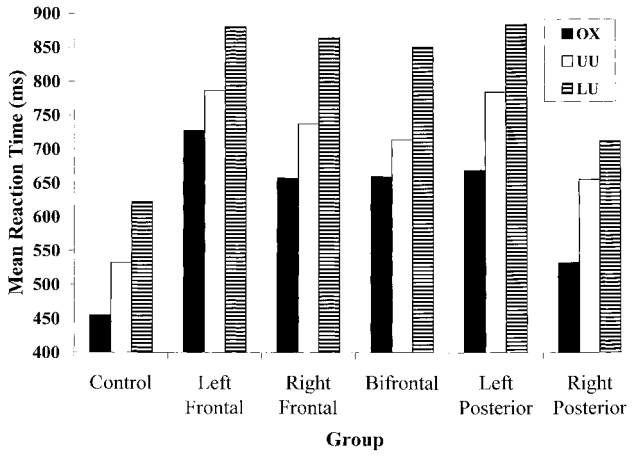

Fig. 4. Mean reaction time to 'Target-Alone' trials as a function of selection task and group.

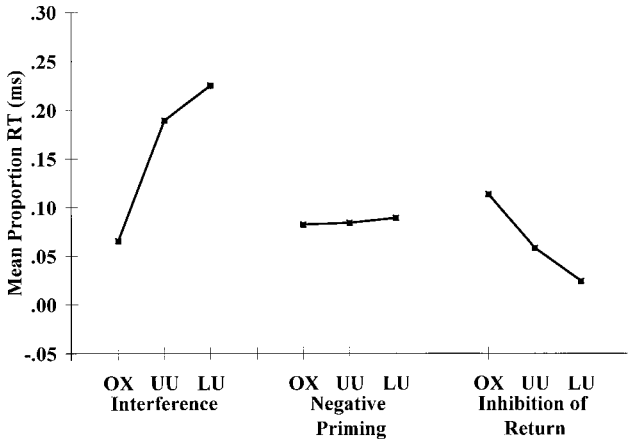

Fig. 5. Proportional measures of performance for the control group on the three measures of attention across the three tasks: OX, UU (upper case–upper case letters), LU (lower case–upper case letters). INT = interference; NP = negative priming; IOR = inhibition of return.

claim concerns the relationship (or lack thereof) between interference and negative priming; we address this relationship below. Others have argued, in contrast to an inhibitory explanation, that negative priming reflects a mismatch between prime and probe displays [33], a process that could reflect episodic retrieval of the previous display [30]. Our data also speak to this issue. Manipulating the complexity of target selection had no influence on proportional measures of negative priming. This is consistent with the notion that NP is a post-selection process, occurring after target selection [23]. That is, unlike the interference measure, negative priming is not sensitive to processes (like cue-target comparisons) required for initial selection, but instead operates after selection has been completed. This theoretical explanation, which has been justified on a number of grounds [23], is consistent with our use of proportional scoring which showed no hint of increasing NP with increasing complexity.

The lack of a task effect may be informative as to the theoretical basis of negative priming. It has recently been argued that, instead of reflecting distractor inhibition, negative priming is due to episodic retrieval of responses made in the prime trial [29]. According to this account, greater negative priming should therefore occur in conditions that encourage such retrieval. One factor that seems relevant here is the similarity of stimuli used in the present prime and probe trials. Although not planned at the outset, our tasks manipulated this factor, in that different target and distractor letters were used on prime and probe trials in the UU and LU tasks, whereas the same two letters ('O' and 'X') were presented on prime and probe trials in the OX task (Figs. 1 and 2). Thus, retrieval of the prime trial should have been greater, or should have occurred more often, in the OX task. However, we found no difference in the proportional magnitude of negative priming across the three tasks. Moreover, absolute difference scoring showed a slight increase in negative priming from OX to UU to LU, a pattern opposite to that predicted by an episodic retrieval account.

An alternative to both the inhibitory and episodic retrieval accounts is that negative priming is due to a mismatch of properties in the prime and probe displays [33]. Based on changes in the prime and probe across tasks (noted above), this account would seem to predict greater negative priming in the UU and LU tasks, as compared to the OX task, because of the greater degree of mismatch in cue, target, and distractor, as well as in their spatial locations. This prediction is suggested by a trend with absolute difference scoring of the present data (a tendency to greater NP with increased task complexity), but not the proportional scoring. As noted by a number of researchers [10], additional research will be required to distinguish these two hypotheses, especially given the possibility that mismatching may occur with regard to perceptual, as well as 'more abstract' (e.g., categorical or response-related), properties [63]. Although not providing definitive data on this debate, our proportional data are consistent with the view that negative priming in the present 'select-what, respond-where' tasks reflects inhibition of spatial selection [59], and that this inhibition does not necessarily depend on the nature of the (within trial) matching process used to identify the target.

One other theoretical issue worth noting concerns the relation between interference and negative priming. Negative priming was initially postulated to reflect an inhibitory process that operated during selection (on the prime trial) to reduce interference from available distractors [28,58]. If this was the case, one should expect a direct relation across subjects between the two measures such that lower levels of interference (i.e., more efficient selection) would be associated with greater negative priming. As with other subsequent studies [23,62], our data do not show such a relationship. At the level of mean task performance, our control subject data show no relation between the two measures in that interference increased across the three tasks (from OX to UU to LU) while negative priming either remained constant (proportional scoring) or slightly increased (absolute difference scoring). More direct correlational analyses across subjects also failed to reveal an inverse relation between the two measures. The correlations for the 19 control subjects between the interference and negative priming measures on OX, UU, and LU tasks were 0.20, −0.23, and 0.06 respectively. This lack of correlation between INT and NP has to be treated with caution. It does not provide evidence that NP is not reflecting an inhibition mechanism selecting the target in the prime display [23]. This argument only follows if inhibition of distractors was the only mechanism of selection. Houghton and colleagues [16] predicted the possibility of positive and negative relationships between INT and NP in a dynamic model of attention. Since these are assumed to be controlled by different neurotransmitter systems, their efficiency could fluctuate independently. Thus NP could still reflect inhibition in selecting target from distractor.

4.3. Inhibition of return

IOR is thought to reflect an attentional bias away from previously examined, but rejected, distractor locations (or objects), a process that would encourage visual scanning for novel locations and objects [40,42,61]. Inhibition of return decreased as a function of target complexity. This suggests that IOR may be

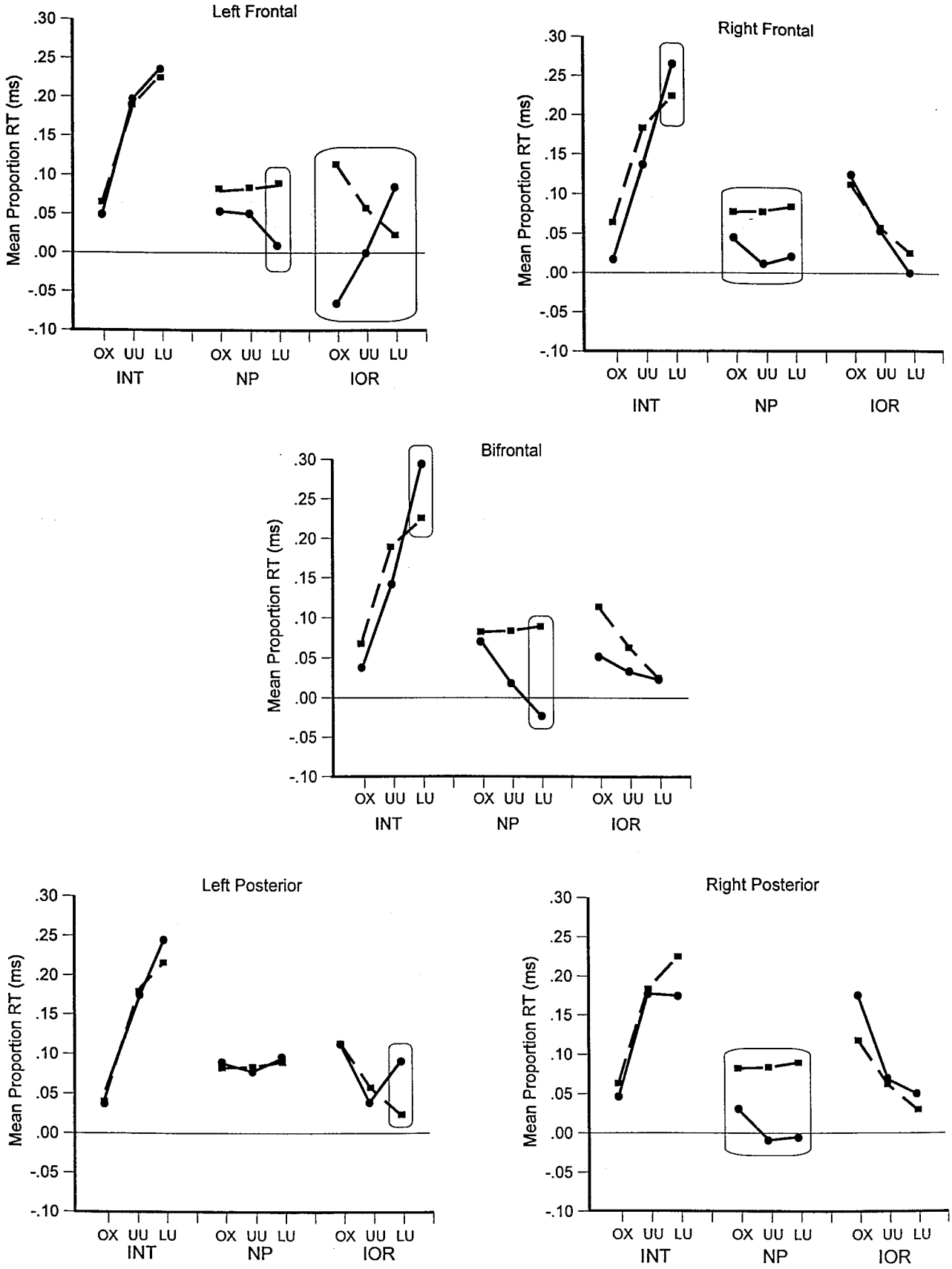

Fig. 6. Profile of performance of the patient groups, each compared to the control group. Control subjects are always presented with dotted lines. INT = interference; NP = negative priming; IOR = inhibition of return; OX; UU = Upper case–Upper case; LU = Lower case–Upper case (see text for definitions). The framed results indicate significant differences.

tied to the strength of the initial (but subsequently suppressed) attentional and/or motoric response to the distractor. Such responses would tend to be large in the OX task where there is an abrupt onset of only one stimulus, the distractor; given that no-go trials were relatively rare in the current paradigm, it is likely this abrupt onset captured attention and produced an initial motoric response that had to be suppressed [31,49]. In the more complex tasks (UU and LU), however, response initiation had to wait on the results of an initial matching stage (see explanation of interference above). If this initial stage failed to result in a match between cue and target, no response would be generated. Note that on the UU and LU distractor-only (no-go) trials, there was still only one potential target location available to summon attention; this may account for why we still continued to find some IOR in these two tasks. The present analysis suggests that such IOR would be reduced further if two or more distractors had been presented on no-go trials.

Regardless of the exact theoretical explanation, the important point is that inhibition of return is modulated by the complexity of target identification and selection. The somewhat paradoxical implication of this result is that inhibition of return is greater with more passive attentional analysis, while more extensive analysis eliminates this effect. Inhibition of return may be an adaptive process that encourages visual scanning of novel locations and objects [18,40]. Along these lines, one might speculate that re-scanning is adaptive under more complex search conditions, such as with multiple-dimension stimuli, perhaps because of the uncertainty of selection (i.e., the possibility of 'being wrong'). Under these conditions, lack of inhibition would allow a more open, flexible readiness to respond to previously non-selected stimuli. This would have an evolutionary advantage. It is also possible that the more complex decisions take longer, which would either mask the inhibition, or perhaps allow it to dissipate.

In summary, in the CTL group, increasing the task difficulty in selection increases the vulnerability to distraction (INT). NP is NOT affected by increasing task complexity, and is consistent with the idea that NP is an index of inhibition. IOR is dramatically altered by task complexity. For the simple selection (OX) task, where there was greater capture of attention and the need for direct motoric suppression, IOR was large; in contrast, when a more active analysis of the target was required (in the UU and LU tasks) there was reduction in IOR, indicating more flexibility in selection. The three patterns of performance of the control participants provide a template with which to interpret the effects of focal brain lesions on the three measures of attention (Fig. 6).

5. Results

5.1. Lesion size

There was no significant group difference in the size of the lesion ($F(4, 23) = 0.507$, $P = 0.731$).

5.2. Patient group analyses

5.2.1. Left frontal (LF) group

The pattern of INT across tasks was virtually identical in the LF and CTL groups, with no significant group or interaction effect. For NP, there was a significant group effect ($F(1,23) = 5.45$, $P < 0.05$), the LF group having an overall significantly diminished priming score. While the interaction was not significant, directed analyses corroborated the visual evidence of less NP with increasing task complexity in the LF group, while the control group did not alter: NP was not significantly different for the two groups in the OX and UU tasks, but was in the LU task ($t(23) = 2.38$, $P < 0.05$). The most dramatic result was the significant interaction for IOR ($F(2,46) = 10.0$, $P < 0.001$). Post-hoc analyses showed significant differences between the two groups in the OX task, where the LF group showed facilitation in selecting a target presented in a previously cued location. The greater IOR for the LF group in the LU task approximated significance ($P = 0.08$). In summary, damage to the left frontal region produced a general impairment of inhibitory processes as indexed by NP and IOR; however, both inhibitory impairments were dependent on task complexity. Moreover, INT, a non-inhibitory measure, showed no impairment, regardless of task complexity.

5.2.2. Right frontal (RF) group

Interference in the RF group showed the same general pattern exhibited by controls—increasing INT with increasing task complexity. The RF group exhibited greater INT than the control group in the most complex task (LU). There was a significant interaction for the INT measure when the OX and LU tasks were directly compared ($F(1,27) = 4.2$, $P = 0.05$). For OX, the RF group revealed less interference, but the same group had more interference on the LU task. The NP comparison revealed no significant interaction, but there was an overall group difference ($F(1,27) = 9.7$, $P < 0.01$) with a decrease in NP for the RF group. Inhibition of return was statistically identical for both groups. In summary, right frontal lobe damage had two effects. First, there was a general decrease in spatial inhibition as measured by NP; but note, however, that there was no difference between patients and controls on the IOR measure, also a measure of spatial

inhibition. Second, there was a greater susceptibility to distracting stimuli with increased task demands (INT).

5.2.3. Bifrontal (BF) group

For the INT score, there was a significant group by task interaction ($F(2,46) = 3.3$, $P < 0.05$) where the BF group had equivalent interference to the CTL group for the two less demanding tasks, but showed significantly greater interference on the most demanding (LU) task. This is similar to the RF pattern. For NP, the BF group revealed decreasing NP with increased task demands. While the group by task interaction for NP did not reveal a significant difference ($F(2,46) = 2.2$, $P = 0.12$), a directed comparison of the two groups for the two most distinct levels of complexity (OX and LU) resulted in a significant group difference for LU only ($t(23) = 3.6$, $P < 0.01$), with diminished negative priming in the BF group. For IOR, there was no significant group or interaction effect. The BF and CTL groups were similar across all tasks, with inhibition decreasing in both groups with increasing task complexity. Thus, the group with bifrontal damage was most similar to the RF group: greater vulnerability to interference (INT) and diminished spatial inhibition (NP), both dependent on task complexity.

5.2.4. Left posterior (LP) group

The LP group showed no significant group or interaction differences from the control group for any measures except for IOR on the most demanding (LU) task, where they revealed an increase in inhibition ($t(24) = 2.1$, $P = 0.05$). The LP group (none of whom had severe aphasia or visual perceptual problems) were thus very similar to the CTL group with one major exception: at the most demanding level of analysis (LU), the normal decreasing IOR pattern was sharply reversed, and the LP group revealed an increase in inhibition just like the LF group.

5.2.5. Right posterior (RP) group

The performance of the RP group on INT was not significantly different from the control group. For NP there was a significant group effect only ($F(1,24) = 12.69$, $P < 0.01$). Analysis of IOR revealed somewhat increased inhibition for the RP group compared to the CTL group, although this did not reach significance. Both groups had the same pattern of decreasing IOR with increasing task complexity. Thus the RP group also differed from the CTL group in only one major regard, but this time on NP. On this spatial inhibition measure, their score was most similar to that of the RF group, although the RP group had somewhat less NP.

5.3. Summary of patient and control group comparisons

The comparison of each patient group with the control group revealed distinct profiles of performance. Interference showed an association with right frontal damage; both the RF and BF (which also had right frontal damage) groups exhibited increased interference, but only in the most complex selection task (LU).

In general, reduced negative priming was associated with unilateral right hemisphere lesions, both the RP and RF groups showing significantly reduced negative priming in all tasks. However, task complexity modulated the pattern of negative priming, with the two other frontal-damaged groups (BF, LF) showing a reduction in negative priming in the most complex selection task (LU). Left posterior damage produced no abnormality in negative priming.

Abnormal response inhibition (IOR) was associated with unilateral left hemisphere lesions, although again the effects were dependent on task complexity. The LP showed increased IOR only with the most demanding task while the LF group showed a reversal of IOR effects across task complexity. These significant results are highlighted by framing in Fig. 6.

6. Discussion of patient group analyses

6.1. Interference

Similar to the control subjects, all patient groups showed the basic (control subject) pattern of increased interference with increased task complexity. A lesion in the right frontal region (right frontal and bifrontal patients) resulted in an elevation of this basic effect under difficult selection conditions.

The proactive-interference hypothesis, reflecting the change from consistently-mapped to variably-mapped targets, proposed for the control subject data likely applies to the patient groups as well for the increase in interference from the OX to UU task. Thus, this interference effect in the patients would be considered 'normal'. In the patients with right frontal lesions (right frontal and bifrontal groups), the additional step from the UU to the LU task resulted in a selective impairment. While these data add further evidence supporting the role of the right frontal lobe in attention [19], our study unfortunately does not allow us to differentiate the reasons for this selective increase in interference. It could reflect a reduced ability to translate from lower to upper case, or an increase in the impact of acoustic confusion. Future research could address this issue by using other types of stimuli.

6.2. Negative priming

The equivalence of NP across task difficulty levels indicated that, in normal individuals, such inhibition is independent of task complexity or difficulty. The complexity of the selection does not influence inhibitory feedback. It is also possible that, for neurologically intact individuals, our task demands were not sufficiently difficult to elicit the functional differences that were more readily apparent in patients with brain damage.

Right hemisphere lesions virtually eliminated negative priming. For the RF and RP groups, the NP scores for all three tasks were not significantly different from zero. At the simplest OX level, the deficit appeared to be greatest for the patients with right posterior lesions. LF patients lose negative priming but only for the LU condition. These results suggest a hierarchical system of organization for attention/inhibition. A relatively passive location-based selection task such as 'OX' might maximally require the RP region, as controlled selection does not have to be performed on each trial. The RF region is possibly not fully recruited at this more automatic level, and would thus generate somewhat more negative priming (as suggested by the figure, but not statistically). As task demands increase, now both the RP and RF (including BF) regions would be needed, and the impairment in negative priming would reflect the involvement of the entire right hemisphere attentional system [15]. At the highest level (LU), the entire frontal lobe is necessary for successful inhibition, as evidenced by a significant impairment for all three frontal groups, now including LF, for the LU task. We cannot determine if this reflects the necessity of additional processes related to different regions of the frontal lobes, or some type of mass effect at a certain level of difficulty or complexity. An interesting possibility, that would need to be further investigated, is that these data reflect a distinction between control processes, and capacity. Regardless, there is ample evidence to indicate greater and more extensive frontal lobe involvement with increasing task demands [55].

NP depends on attentional resources. NP has been reported to decrease as workload, related to attentional resources, increases [9]. Our results extend that concept. NP does decrease with increased attentional requirements, but only if the attentional system is damaged, or if the task is sufficiently complex. NP is resource, task and brain system related, in an interactive manner. If other than spatial attention tasks are used, it is possible that a different attentional brain system would be affected [61]. For example, if the task had been related to naming, then temporal areas necessary for identification would be more involved. At the highest task demands, all frontal regions appear to be required, and this would likely be independent of task content.

The support in our study for the dissociation of NP and INT was first evidenced in the control subject data and is now strengthened by the patient group data. Two sources of evidence from the patient data support the dissociation of these measures. First, lesions in separate neural regions differentially affect INT and NP. Interference is increased by lesions that involve the right frontal region only (RF and BF groups). Negative priming is affected by right hemisphere lesions, including the RP. Second, the correlations between NP and INT for the patient groups in all three tasks were not significant ($P > 0.2$). The INT and NP measures are clearly dissociable, since they are differentially affected by lesion site and task demand, and in addition are not correlated in control or patient groups. These results are consistent with the dynamic model of attention proposed by Houghton and colleagues [16].

6.3. Inhibition of return

There were significant differences in IOR only in the patients with left hemisphere lesions. In particular, the LF group's results are striking, with a paradoxical opposite pattern to the CTL group. This group exhibits no response inhibition at the simplest OX level; in fact, the speed of response is facilitated. This may reflect Luria's [22] concept of the importance of the left frontal regions for motor control. That is, with left frontal damage, there is loss of response inhibitory control. A more compelling explanation derives from the concept of motor capture errors ([43], pp. 328–345). Patients with left frontal lesions not only cannot easily suppress a motor response to a location previously suppressed in a passive attentional task, but their attention has been captured and subsequent responses to this location are facilitated, with faster RT.

There is a dissociation noted within the left hemisphere when the two left hemisphere groups were directly compared. For the OX task, while the LF group had decreased IOR, the LP group performed identically to the CTL group on IOR. On the most demanding LU task, on the other hand, the two left hemisphere groups both revealed increased IOR, in contrast to all other groups. This was evident in a direct two group (LF, LP) by task (OX, UU, LU) analysis; $F(2,22) = 3.8$, $P < 0.05$. Significant post hoc differences were observed only for OX, with the LU comparison being $F < 1$. The LU task requires the greatest active analyses, including perceptual match/mismatch; letter analysis; and overcoming phonemic/acoustic confusion.

If more active analysis normally leads to less response inhibition and greater flexibility and openness

(as suggested above in the CTL data) in order to meet greater environmental demands, the two left hemisphere groups appear to be less flexible in these circumstances. This clearly would have significant impact on their daily behaviour. The left frontal group is doubly affected—they are captured in passive attentional motor tasks; they are less flexible in more demanding attentional tasks. With the more demanding task, the entire left hemisphere works (or does not work efficiently) in conjunction. The left frontal lobe seems to play an important role in the suppression of inappropriate motor responses (motor capture errors) in more automatic motor tasks. If damaged, there will be no overriding inhibition of the response to a salient trigger, and the motor response schema are activated inappropriately [31,43]. The IOR deficits of the left frontal group in the OX task could also be described as a tendency to perseverate due, not to a failure to suppress a previous response, but to an over-excitation leading to facilitation.

Based on observed abnormalities on inhibition of return in patients with progressive supranuclear palsy, Posner et al. [41] identified the superior colliculus as a probable locus for this measure. They also demonstrated normal IOR in patients with Parkinson's disease, and in patients with lesions in frontal, parietal, or temporal lobes. However, many of the attentional deficits following brain injury may only be observed under difficult selection conditions, as our data suggest. Also, the frontal patients in Posner et al.'s research may not have had lesions in areas similar to our patients.

The absolute mapping of this 'motor capture error' to the left frontal region is still premature, since we did not control for response hand. It is possible that these results reflect the impaired control by the left frontal region of the contralateral hand, rather than a functional motor control dominance.

Since the frontal lobes are involved with working memory, it might be hypothesized that the observed results, particularly with increasing task complexity, were related to a deficit in working memory. This is unlikely for the main reason that performance was not impaired in numerous conditions, including the most difficult task level. Thus, the LF group showed no deficits in INT across the three levels of task difficulty, and the two other frontal groups revealed no deficits in IOR across these three tasks. A working memory, or even instructional-set deficit, hypothesis would predict deficits for all tasks at the most complex level.

7. General discussion

Several general conclusions may be drawn from these data. The first general conclusion is that in normal subjects there is a dissociation of measures of interference, negative priming, and inhibition of return as a function of task complexity. Second, the patient data support these dissociations by demonstrating that pathology in specific brain regions differentially affect the various measures. Thus selectivity in attention is a result of a complex interaction of several different processing mechanisms, and potentially different brain regions [16,25,26,39]. Mesulam [26] has suggested that the complex behaviour of attention is based on neural networks that facilitate rapid and versatile computational processing. Our results agree with this general statement and specify to some greater degree the anatomical and functional specificity of these networks.

Third, our results clarify the role of the frontal lobes in anterior attentional processes, with evidence of specific functional localization. The right frontal lobe is most detrimentally affected by the presence of distracting stimuli. Other data indicate caution, replication, and extension at this stage of specificity in localization. PET studies suggest a non-hemisphere specific effect of the medial frontal regions [11,36,64]. Behavioural studies also do not present a coherent location picture. The right dorsolateral frontal zones have been implicated in selective attention/inhibition [2,19,20,67], directed attention to extra personal space [15,49], and sustained attention [13,65]. Other behavioural data indicate a non-hemisphere specific role for the medial frontal area [1,17,21,51]. These differences may be related to a functional dissociation between dorsal and ventral anterior cingulate regions. There are cautions related to these observations. While we tried to minimize the effects of etiology, our emphasis on single focal circumscribed lesions did result in patient groups with varying etiologies. Lesion size was not a factor in our study, but several scans had not been available for quantification. One conclusion is clear—the investigation of the specificity of the frontal lobes in attentional processes and the organization of attentional systems will require many patients with clearly localized lesions and defined cognitive processes.

The IOR results in the left frontal patients have the greatest potential implications for real-life behaviours. The IOR measurement normally indexes the continuing suppression of a location to which a first response was not made. The control subject study revealed an interaction with task complexity, facilitation of response speed demonstrated at the most complex levels. Patients with left frontal damage had a pattern of response that was opposite to that of the CTL group, and most other patient groups. Patients with left frontal damage are compromised in life at all levels of task complexity, at least for this type of task.

Our data not only indicate considerable specificity of anterior attentional systems, but also an interaction

between the two related to task demands. Cognitive theories emphasizing 'control-automatic' dissociations provide a general approach to frontal/posterior functional interactions, but they do not capture the complexity. Evidence as to how 'control' and 'automatic' processes might differ depending on even slight changes in task demands was provided by Winocur et al. [66]. Word stem completion and word fragment completion are considered to provide measures of implicit (automatic, non-conscious) memory. Yet these two measures can be dissociated based on task demands. Reduced priming (implicit memory) on word stem completion is secondary to some level of disturbed control, and was related to frontal lobe dysfunction, while another implicit memory measure (word fragment completion) was not.

Shimamura [47] has proposed that frontal dysfunction could be reduced to a failure of inhibitory processes, and that any localization/functional differences within the frontal lobes could be attributed to the interconnectivity of the frontal lobes with functionally distinct posterior brain regions; the frontal lobes serve to inhibit these different posterior modular processes. This concept is similar to Denny-Brown's [7] view of interaction between frontal inhibitory and parietal exploratory tendencies to explain exploratory (frontal lesions decrease inhibitory control) or repellent (frontal inhibition stronger than damaged parietal exploratory functions) abnormal behaviours. Our results suggest a more complex interplay. Inhibition is not simply a function of the frontal lobes, with inhibition (or impairment of inhibition) being demonstrated in patients with frontal or posterior lesions, depending on task complexity. There is also evidence that, depending on task demands, facilitation within the frontal lobes may occur. Both excitation and inhibition, facilitation and suppression, are necessary and are dependent on task demands. The interaction of these inhibitory and excitatory processes must be taken into account in the complexity of brain functioning. We suggest that tasks with different cognitive demands beside spatial location and a greater range of complexity be used to examine if even finer distinction of attentional processes and greater specificity of brain correlates may be revealed.

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Appendix A

Mean interference for prime, probe and proportional reaction times (ms) as a function of task and group.

		O–X			Upper case–Upper case			Lower case–Upper case		
		Target alone	Target + distractor	Proportion	Target alone	Target + distractor	Proportion	Target alone	Target + distractor	Proportion
Control	*M*	454.74	484.00	0.065	532.32	632.37	0.189	622.05	762.74	0.225
	SD	65.90	69.68	0.046	63.69	83.56	0.081	95.44	132.45	0.078
Left frontal	*M*	727.00	753.17	0.050	785.33	942.67	0.200	880.50	1089.33	0.230
	SD	201.74	160.94	0.070	140.53	192.64	0.050	143.75	239.99	0.150
Right frontal	*M*	657.00	661.80	0.013	737.00	835.20	0.134	863.10	1090.80	0.263
	SD	144.02	133.37	0.064	128.54	151.11	0.065	190.91	271.99	0.141
Bifrontal	*M*	658.83	679.67	0.037	713.33	804.67	0.142	849.33	1111.00	0.299
	SD	173.67	164.14	0.060	184.08	169.58	0.087	198.83	323.51	0.113
Left posterior	*M*	668.29	708.00	0.062	783.57	917.71	0.180	883.00	1111.29	0.244
	SD	259.74	285.23	0.061	241.42	270.28	0.119	263.81	384.04	0.124
Right posterior	*M*	532.00	554.71	0.040	654.71	776.57	0.190	711.71	842.43	0.190
	SD	68.90	76.52	0.040	96.78	147.84	0.130	73.26	82.17	0.070

Appendix B

Mean negative priming for prime, probe and proportional reaction times (ms) as a function of task and group.

		O–X			Upper case–Upper case			Lower case–Upper case		
		Control	Ignored repetition	Proportion	Control	Ignored repetition	Proportion	Control	Ignored repetition	Proportion
Control	*M*	455.74	491.74	0.080	633.95	685.05	0.080	754.16	819.37	0.090
	SD	72.12	69.61	0.040	82.16	93.35	0.100	123.59	132.46	0.070
Left frontal	*M*	695.50	725.67	0.050	913.33	954.33	0.050	1118.17	1127.00	0.010
	SD	136.39	110.95	0.070	217.84	211.78	0.060	221.20	239.01	0.080
Right frontal	*M*	719.10	748.80	0.050	951.30	944.00	0.010	1092.30	1119.70	0.030
	SD	231.66	218.92	0.080	238.69	160.22	0.100	301.15	276.16	0.080
Bifrontal	*M*	664.00	708.00	0.074	906.00	908.67	0.020	1138.17	1123.33	−0.020
	SD	202.71	215.27	0.040	310.47	284.13	0.090	385.53	430.00	0.050
Left posterior	*M*	656.14	702.71	0.090	895.57	972.29	0.080	1129.57	1219.57	0.090
	SD	275.87	254.19	0.090	270.84	331.47	0.090	459.70	474.37	0.100
Right posterior	*M*	567.14	577.43	0.030	810.14	798.29	−0.010	889.57	881.14	0.000
	SD	97.44	74.48	0.070	175.17	161.55	0.110	124.86	114.67	0.080

Appendix C

Mean inhibition of return for prime, probe and proportional reaction times (ms) as a function of task and group.

		O–X			Upper case–Upper case			Lower case–Lower case		
		Uncued	Cued	Proportion	Uncued	Cued	Proportion	Uncued	Cued	Proportion
Control	*M*	429.58	475.16	0.113	509.32	538.32	0.058	573.84	584.84	0.024
	SD	59.42	62.90	0.117	60.11	64.85	0.051	87.32	75.61	0.060
Left frontal	*M*	669.83	623.33	−0.060	738.33	738.00	0.000	774.83	838.33	0.080
	SD	156.50	126.26	0.060	133.72	135.32	0.040	153.73	175.64	0.100
Right frontal	*M*	609.80	678.40	0.124	708.30	742.30	0.049	892.00	883.60	−0.001
	SD	128.89	151.98	0.192	111.79	112.68	0.038	237.12	200.91	0.081
Bifrontal	*M*	630.83	639.67	0.046	629.83	645.83	0.032	780.50	802.67	0.022
	SD	173.32	100.60	0.173	160.34	144.06	0.055	185.10	219.43	0.058
Left posterior	*M*	619.71	692.57	0.112	747.57	779.57	0.038	792.29	861.00	0.090
	SD	207.13	242.95	0.122	236.73	263.42	0.038	226.36	252.13	0.099
Right posterior	*M*	497.43	585.57	0.159	622.43	656.86	0.061	678.43	700.86	0.057
	SD	91.23	104.79	0.084	132.37	117.61	0.078	114.35	75.61	0.089

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