

Response Channel Activation and the Temporoparietal Junction

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When we learn to make one motor response to one visual stimulus and a different motor response to another, representations of these stimulus–response associations must be maintained to efficiently transduce perception into action. When an irrelevant distractor is presented adjacent to a target stimulus, interference is observed when the two stimuli are associated with conflicting responses, presumably due to response channel activation by the incompatible information. We have explored the neural bases of these interference effects. In a previous study, patients with hemispatial neglect showed normal interference from contralesional flankers. In another study, patients with lesions of the lateral prefrontal cortex were found not to show interference from distractors presented in the contralesional hemifield. The current study provided a more anatomically detailed investigation of the effects of posterior association cortex lesions on flanker interference. Patients with chronic, unilateral lesions involving the temporoparietal junction (TPJ), two of whom had hemispatial neglect, were compared with patients with lesions of the posterior association cortex not involving the TPJ. All patients performed a color discrimination task at fixation while a congruent or incongruent colored flanker was briefly presented (16.7 ms) in the adjacent contralesional or ipsilesional hemifield. Patients with TPJ lesions showed no interference effects from the contralesional flankers. These results suggest that the TPJ, in combination with the dorsolateral prefrontal cortex, is involved in transducing perception into action. © 1998 Academic Press

Although patients with hemispatial neglect frequently fail to report stimuli from their contralesional hemifields, it is now well established that this neglected information often undergoes extensive perceptual processing. Volpe, Ledoux, and Gazzaniga (1979), for example, demonstrated that patients with

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neglect were better than chance when asked to guess whether two stimuli were the same or different. The better than chance performance in these patients occurred even though the patients denied awareness of the contralesional stimulus. Subsequent studies have now provided evidence that neglected stimuli can be processed even up to lexical and semantic levels (Berti & Rizzolatti, 1992; Ladavas, Paladini, & Cubelli, 1993; McGlinchey-Berroth, Milberg, Verfaellie, Alexander, & Kilduff, 1993).

Audet, Bub, and Lecours (1991) investigated implicit processing with the flanker task, first introduced by Eriksen and Eriksen (1974; Taylor, 1977). In this task, subjects make a choice response based on a property of a central target (e.g., 'X' or 'O'). The target is flanked by irrelevant stimuli that are congruent, incongruent, or neutral to the target. For example, if the target is an X, the flankers would be X, O, or N for the congruent, incongruent, and neutral conditions, respectively. In the Audet et al. study, a single irrelevant flanker was always presented contralesional to a target stimulus. Two neglect patients were tested, both of whom reported no awareness of the flankers. Despite this lack of awareness, one of the patients showed interference from contralesional flankers. Moreover, the magnitude of this interference was equal to the size of interference when the flankers were presented above the target, an arrangement in which the patients were aware of the irrelevant distractors. The second patient, however, did not show any interference from contralesional distractors.

Cohen, Ivry, Rafal, and Kohn (1995) used a different variant of the flanker task in a study with two hemispatial neglect patients. On each trial, the patients performed a color discrimination task on a target stimulus presented at fixation. Simultaneous with the target, an irrelevant colored stimulus was presented in either the contralesional or ipsilesional hemifield. Both patients displayed interference that was equal in magnitude between the contralesional and ipsilesional hemifields. They concluded that flanker interference did not require awareness and it was suggested that flanker interference is not mediated by neural structures located in the posterior association cortex.

The finding that some neglect patients show flanker interference from contralesional stimuli is important in demonstrating the extent of implicit processing in the absence of awareness. What remains unresolved is which neural structures are involved in generating flanker interference effects. To address this question, Rafal, Gershberg, Egly, Ivry, Kingstone, and Ro (1996) tested patients with unilateral lesions of the lateral prefrontal cortex. The study was motivated by the assumption that flanker interference is primarily due to response channel activation and response competition effects. Because the flanker task usually requires an arbitrary stimulus to response mapping (e.g., mapping colors to response keys), it was hypothesized that frontal patients would show a deficit in maintaining these arbitrary mappings. This assumption, mainly derived from neurophysiological studies implicating the prefrontal cortex as being involved in working memory (Wilson,

Scalaidhe, & Goldman-Rakic, 1993), seemed reasonable since in addition to examining the properties of visual selective attention, the flanker task has also been noted to involve response related processes (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Eriksen, Coles, Morris, & O'Hara, 1985; Eriksen & Schultz, 1979; Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). As predicted, patients with prefrontal lesions showed a reduced flanker interference effect. Notably, the attenuated effect was only observed for contralesional flankers; when the flanker appeared in the ipsilesional hemifield, the magnitude of the effect was similar to that observed in age-matched controls. From this study, it was concluded that the lateral prefrontal cortex is involved in transducing perception into action.

The current investigation was conducted to provide a more careful examination of other anatomical regions that may underlie the flanker effect. Since the flanker task is a multicomponent task that involves visual information processing, visual selection, as well as response-related processes such as maintaining arbitrary stimulus-response mappings, it seems reasonable to assume that other brain areas could also be involved in flanker interference effects. In particular, we tested patients with lesions in the posterior association cortex. We were mainly interested in lesions that involved both the inferior parietal lobule and the superior temporal gyrus (temporoparietal junction or TPJ). This interest was based on results demonstrating the importance of these areas in generating the P300 component of the event-related potential (Knight, Scabini, Woods, & Clayworth, 1989), which has been shown to be related to stimulus evaluation processes underlying the flanker interference effect (Coles et al., 1985), and in disengaging spatial attention (Friedrich, Egly, Rafal, & Beck, 1998). We compared a group of these patients in whom the lesion involved the TPJ with a group of patients in whom the lesion spared the TPJ. The TPJ group included two patients with chronic hemispatial neglect. The motivation for including patients with neglect was to help clarify discrepancies from earlier studies, as discussed above, and to further examine how consistently neglect patients show interference from contralesional flankers.

METHOD

Patients

Twelve patients with chronic, unilateral lesions of the posterior association cortex participated after giving informed consent. Six of the patients had lesions involving the temporoparietal junction (TPJ group) and the other six patients had lesions of the posterior association cortex sparing the TPJ (non-TPJ group). Eight of these 12 patients, 4 from each group, had also participated in the study by Friedrich et al. (1998). The magnetic resonance images and/or computerized tomographic images of the patients were used to transform their lesions onto standardized transaxial templates and were subse-

quently registered and reconstructed using a computerized method (Frey, Woods, Knight, & Scabini, 1987). The group-averaged reconstructions for the patients in each lesion group are shown in Fig. 1. The individual reconstructions for each patient are shown in Figs. 2a and 2b for the TPJ group and the non-TPJ control group, respectively. Details of each patient are given in Table 1.

Two of the TPJ patients, SD and EN, had chronic hemispatial neglect, as confirmed by reliable extinction on confrontation testing, line cancellation and bisection tasks, and by their performance in other experiments (Ro & Rafal, 1996; Rorden, Ro, Robertson, Mattingley, & Driver, 1997). SD suffered two strokes involving the posterior branches of the right middle cerebral artery. The first stroke involved the inferior, middle, and superior temporal gyri, the supramarginal and angular gyri, and the superior parietal lobule. The second stroke extended the infarct to involve more of the sensory, motor, and dorsolateral prefrontal cortex and left her with a left hemiplegia and hemianesthesia. Patient EN suffered a stroke in the distribution of the right middle cerebral artery. His lesion involved the middle and superior temporal gyri, the angular and supramarginal gyri in the inferior parietal lobule, and extended anteriorly to include sensorimotor cortex and the dorsolateral prefrontal cortex (see Table 1 and Fig. 2a). As the lesions of both neglect patients spared the occipital cortex, SD and EN had no visual field deficits. None of the other chronic patients in this study had residual clinical neglect or extinction nor visual field defects. Note that the two patients with neglect also had lesions with the largest volume.

Apparatus

All patients except for the two neglect patients and patient AR were run on an IBM-compatible, personal desktop computer that was connected to a NEC Multisync video graphics array (VGA) monitor. The two neglect patients and patient AR were run on a Toshiba T4400C IBM-compatible laptop computer with an active matrix color, VGA stimulus monitor. In both cases, the graphics mode was set to a 640×480 pixel resolution using Borland's Graphics Interface. Because the laptop monitor was smaller than the desktop monitor, the number of pixels used for the stimuli was adjusted so that the visual angles remained constant. On both computers, the timing of the visual displays was synchronized with the vertical synchronization of the computer monitors at 16.7 ms intervals (60 Hz). Millisecond (ms) timing, used to obtain response latencies, was accomplished by setting the 8253 chip of the computers to millisecond ticks. Responses were made on a two-button joystick connected to the gameport adapter when a desktop computer was used and on a two-button mouse connected to the serial adapter of the computer when testing was conducted with the laptop. Response times were recorded to the nearest millisecond.

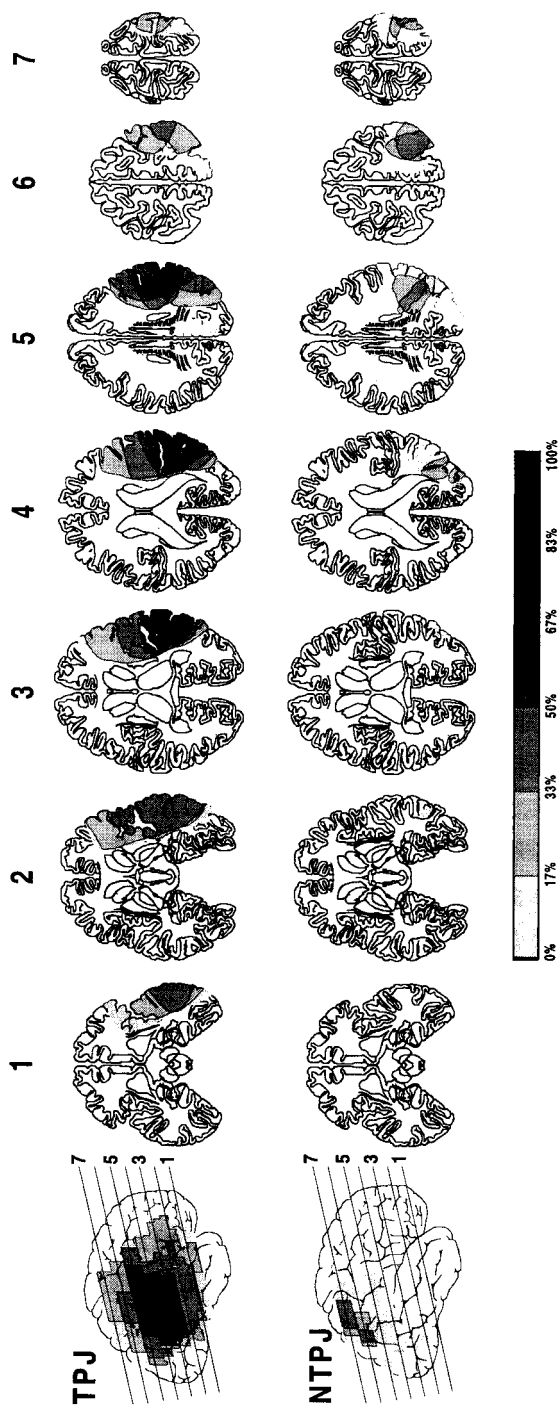


FIG. 1. Neuroimage reconstructions for the two patient groups. The top row represents the percentage of lesion overlap for patients in the TPJ group and the bottom row for patients in the non-TPJ control group. All lesions were reconstructed onto the right hemisphere of the brain for this figure. The lesions depicted on the lateral views also include the underlying white matter.

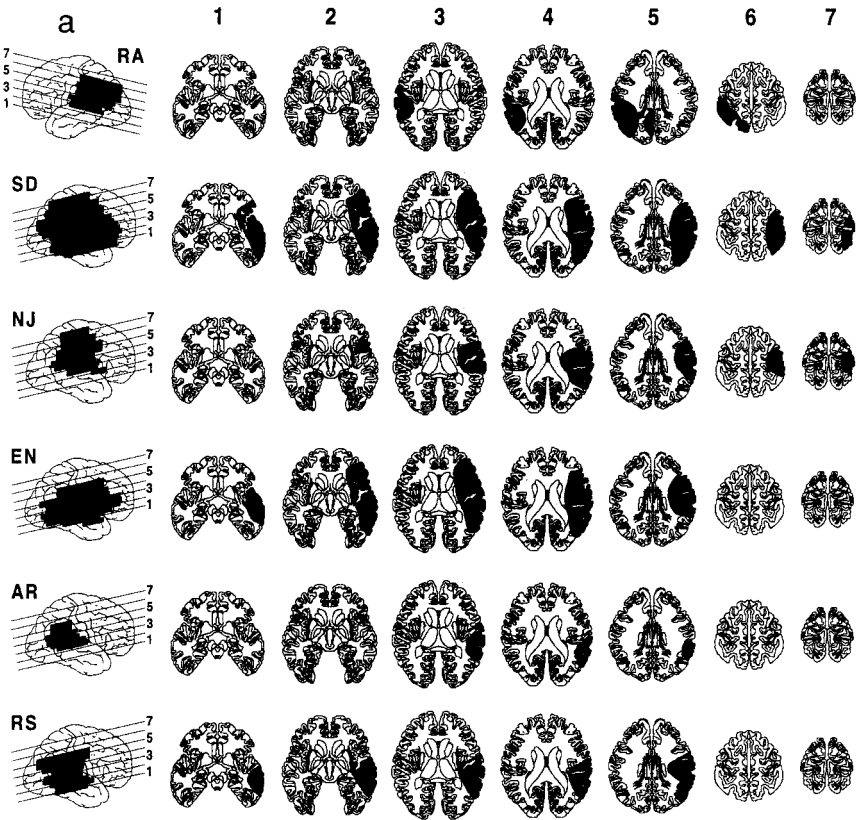


FIG. 2. (a) The individual neuroimage reconstructions for each patient in the TPJ group. (b) The individual neuroimage reconstructions for each patient in the non-TPJ control group.

Stimuli and Procedures

All of the stimuli used in this experiment were presented on a black background. The fixation point was a small gray circle measuring 0.1° . The targets and flankers were filled, colored squares measuring 1° in the horizontal and vertical directions. The targets and flankers were either red or green with equal probability. Thus on half of the trials, the flanker was congruent with the target and on the other half it was incongruent. The center-to-center distance between the target and the flanker was 3° .

The fixation point appeared at the start of each trial in the center of the computer monitor and was presented for 500 ms before the onset of the target and flanker display. Following the 500-ms fixation interval, a red or green color target stimulus appeared on top of the fixation point. A peripheral distractor stimulus simultaneously appeared either to the left or to the right of

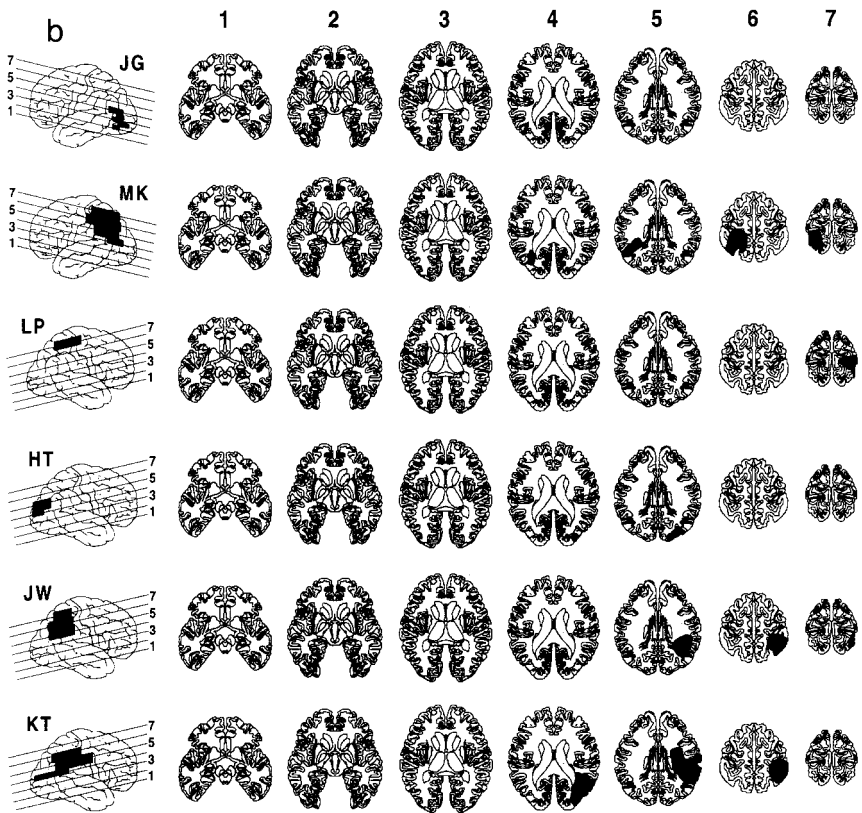


FIG. 2. *Continued*

the central color patch. The peripheral color patch was presented for 16.7 ms and the central color patch was presented until a response was made.

The patients sat approximately 57 cm from the computer monitor. They were instructed to respond to the central target by pressing one button on the response pad if the target was red and the other button on the response pad if the target was green. They were instructed to ignore the flanker that flashed in either the contralesional or ipsilesional hemifield. The patients used the index and middle fingers of their ipsilesional hand to respond. The subjects were instructed to respond as fast and as accurately as possible. Trials with incorrect responses and responses faster than 150 ms or slower than 2500 ms were discarded from the analysis of reaction times (RTs).

All of these same patients also performed a peripheral report task of this experiment in which they were instructed to respond to the briefly presented, peripheral color patch in the same manner as in the main task. In this peripheral report task, however, it was the center distractor that remained present

TABLE 1
Patient Information

Patient	Age	Sex	Neglect	Clinical	Lesion information			
					Hemisphere	Volume ^a	Vintage ^b	Etiology
RA	64	M	-	A	Left	77	6	Stroke
SD	61	F	+	G	Right	195	2	Stroke
NJ	70	M	-	A	Right	80	7	Stroke
EN	52	M	+	H	Right	149	1	Stroke
AR	56	M	-		Right	26	2	Stroke
RS	50	M	-		Right	80	5	Stroke
TPJ mean	58.8					101.2	3.8	
JG	64	M	-		Left	4	3	Stroke
MK	50	M	-		Left	33	28	Shrapnel
LP	71	M	-		Right	6	5	Stroke
HT	83	M	-		Right	8	3	Stroke
KT	47	F	-	H	Right	46	17	Tumor
JW	74	M	-		Right	26	7	Stroke
Non-TPJ mean	64.8					20.5	10.5	

Note. A, aphasia; H, hemiparesis; G, hemiplegia.

^a Volume in cc.

^b Vintage in years.

until a response was made and the peripheral target was only visible for 16.7 ms. Because of the brief exposure of the target stimulus, many of the subjects had difficulty with this task. This was especially problematic for the two neglect patients, who were either at chance when attempting to guess the color of the target when it was contralesional (SD) or did not respond to any of the contralesional target trials (EN). Because of the high number of errors the patients made, and also because of the differences in target duration and fixation introduced by this procedure, the data from this peripheral report task are not reported.

Design

Each patient first completed a practice block of 16 trials. Following the practice block, a total of 96 trials was collected from each patient, 24 for each of the four within-subject conditions: 2 levels of flanker congruency (congruent vs. incongruent) \times 2 levels of field (contralesional vs. ipsilesional). Patient group (TPJ vs. non-TPJ patients) served as the between-subject factor.

RESULTS

The RT data from the correct responses for every patient in each condition were first trimmed by removing all outliers that were more or less than 2

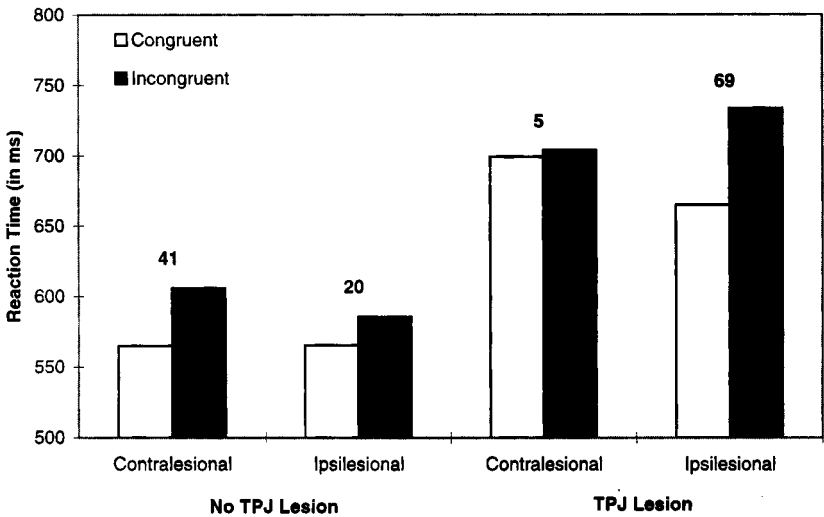


FIG. 3. The data from the central report task are shown here for each patient group. The light bars represent the mean latencies for flanker congruent trials and the dark bars represent the mean latencies for flanker incongruent trials. The left pair of bars for each patient group are for flankers that were presented contralesionally and the right pair of bars for ipsilesional flankers.

standard deviations (SD) from the mean. Along with the error trials, this trimming procedure resulted in the elimination of a total of 6.9% of the trials. The error data were not further analyzed.

The means of the remaining RTs were then subjected to a three-way analysis of variance (ANOVA). Patient group served as the between-subject factor. Congruency and field of flanker served as the two within-subject factors. The group averaged data from this analysis are shown in Fig. 3 and the data for each patient in each condition are presented in Tables 2a and 2b. There was a significant main effect of flanker congruency, with RTs being slower when the flanker was incongruent with the target response [$F(1, 10) = 8.91, p < .02$]. There was also a significant patient group \times congruency \times field triple-order interaction [$F(1, 10) = 5.10, p < .05$]. All other main effects and interactions did not approach significance [all $ps > .20$].

Planned comparisons were performed separately on the data from the two patient groups. In the TPJ patients, the main effect of congruency was marginally significant [$F(1, 5) = 5.64, p = .06$], as was the congruency \times field interaction [$F(1, 5) = 5.66, p = .06$]. Paired t tests of the congruency effects within each hemifield of the TPJ patients revealed that the source of this marginally significant interaction was due to a significant flanker interference effect from ipsilesional flankers [$t(5) = 3.78, p < .02$], but a lack of flanker congruency effects with contralesional flankers [$t(5) = .21$]. In the non-TPJ

TABLE 2a

Mean RTs, Standard Deviations (SD), and Percentage of Error Including RT Outliers for the Different Conditions for Each Patient in the TPJ Group

Patient		Contralesional flanker		Ipsilesional flanker	
		Congruent	Incongruent	Congruent	Incongruent
RA	RT	637	713	681	753
	SD	92.1	122.7	88.4	85.1
	% Error	4.2%	8.3%	4.2%	8.3%
SD	RT	919	833	769	856
	SD	175.0	192.3	99.4	123.7
	% Error	8.3%	12.5%	12.5%	12.5%
NJ	RT	769	798	708	831
	SD	143.7	101.2	104.7	167.8
	% Error	4.2%	8.3%	8.3%	0.0%
EN	RT	941	965	920	1022
	SD	196.0	234.0	192.3	260.4
	% Error	12.5%	8.3%	16.7%	29.2%
AR	RT	441	453	441	459
	SD	36.3	44.3	41.0	52.4
	% Error	8.3%	12.5%	4.2%	4.2%
RS	RT	488	461	469	483
	SD	115.0	87.0	119.9	101.7
	% Error	4.2%	4.2%	4.2%	8.3%
	TPJ mean	699	703	665	734
	SEM	48.5	47.6	87.1	74.5
	% Error	6.9%	9.0%	8.3%	10.4%

Note. The group standard error of the mean (SEM) is presented at the bottom of the table. Note that the overall slower response times for this group are mainly due to the two neglect patients.

patients, only the main effect of congruency approached significance [$F(1, 5) = 3.48, p = .12$]. The congruency effect in the non-TPJ patients did not achieve significance because of one patient showing a reversal in RT performance in the ipsilesional hemifield and another patient showing a reversal in the contralesional hemifield (see Table 2b).

Further planned comparisons were conducted to determine the difference in performance between the two patient groups within each hemifield. An ANOVA with congruency and patient group was conducted on the data from the contralesional flanker trials. None of the main effects or interactions approached significance in this analysis [all $ps > .15$]. When this same ANOVA was conducted on the data from the ipsilesional flanker trials, however, a marginally significant congruency \times patient group interaction was present [$F(1, 10) = 3.95, p = .07$]. This interaction was driven by a larger interference effect in the ipsilesional hemifield of the patients with TPJ lesions.

TABLE 2b
The Data from the Non-TPJ Patient Group

Patient		Contralesional flanker		Ipsilesional flanker	
		Congruent	Incongruent	Congruent	Incongruent
JG	RT	539	576	586	540
	SD	71.1	110.9	75.8	66.7
	% Error	4.2%	0.0%	4.2%	4.2%
MK	RT	455	575	459	474
	SD	71.6	124.9	73.3	79.6
	% Error	8.3%	4.2%	4.2%	8.3%
LP	RT	516	581	512	554
	SD	54.5	62.3	56.0	77.1
	% Error	8.3%	8.3%	8.3%	12.5%
HT	RT	786	791	781	795
	SD	153.0	162.5	151.1	84.2
	% Error	4.2%	4.2%	0.0%	4.2%
KT	RT	600	672	574	652
	SD	125.2	127.2	71.7	127.0
	% Error	4.2%	4.2%	4.2%	4.2%
JW	RT	494	440	481	497
	SD	105.9	72.2	105.9	101.4
	% Error	4.2%	8.3%	0.0%	4.2%
	Non-TPJ mean	565	606	565	585
	SEMs	47.8	48.8	84.8	90.6
	Errors	5.6%	4.9%	3.5%	6.2%

DISCUSSION

In this study, patients with lesions of the temporoparietal junction failed to demonstrate flanker interference effects when the flankers were presented in the contralesional hemifield. This group did show a substantial flanker effect when the peripheral distractor was presented in the ipsilesional hemifield. Moreover, the mean RTs for both the congruent and incongruent conditions in the contralesional condition fell between these values for the ipsilesional condition. This suggests not only that there were no effects of these contralesional flankers but also that there was both facilitation from identical distractors and inhibition from response incongruent distractors in the ipsilesional hemifield. The large ipsilesional flanker effects in the TPJ patients, as compared to the congruency effects demonstrated from the patients with lesions sparing the TPJ, may be due to a hyperorienting response towards the ipsilesional hemifield (Kinsbourne, 1993; Seyal, Ro, & Rafal, 1995).

The findings of the current study are similar to those previously reported in patients with lesions of the lateral prefrontal cortex (Rafal et al., 1996). In both investigations, no interference was observed when incongruent distractors were presented to the contralesional hemifield. The similar results

with these two patient groups suggest that these areas are part of a network contributing to the transduction of perception into action. The temporoparietal junction may be more involved with stimulus evaluation components of this task and the lateral prefrontal cortex with the actual transduction and maintenance of the arbitrary response mappings. The results demonstrating TPJ involvement in generating the P300 component of the event-related potential (Knight et al., 1989) and prefrontal cortex involvement with working memory (Wilson et al., 1993) are consistent with this interpretation.

Two of the TPJ patients in this study had neglect. These patients also demonstrated large ipsilesional flanker effects and either no flanker effect (patient SD) or an attenuated effect (patient EN) in the contralesional condition. Lavie and Robertson (1997) have recently reported a related study of flanker interference in neglect patients. They included a manipulation of perceptual load; previous work had shown that when load is high, the magnitude of flanker interference is reduced (Lavie, 1995; Lavie & Tsai, 1994). The patients studied by Lavie and Robertson also showed less interference from contralesional flankers. Since patients with neglect often have large volume lesions, the lack of or reduced flanker effects in the contralesional field could simply be due to a lesion size effect.

Overall, the patients in the TPJ group of the current study had larger lesion volumes than the patients in the non-TPJ control group. It may be that lesion size, rather than lesion location, is more important in determining whether response channel activation occurs. Correlations between the lesion volume and the magnitude of the flanker effect were calculated to determine whether the size of the lesion influenced the observed results. Over the 12 subjects, lesion size was substantially correlated with the magnitude of the interference effect. For contralesional flankers, the correlation between lesion size and flanker effect was -0.44 and was $.67$ for ipsilesional flankers. Both of these correlation values are substantial and in the predicted direction, but may be biased by the fact that the patients with TPJ lesions had larger lesions. Nonetheless, the correlations suggest that lesion size may also be a contributing factor in response channel activation. Further research is necessary to clarify the role of lesion size in distractor interference effects.

These results may superficially appear to be in opposition to those reported by Cohen et al. (1995). All three¹ of the patients studied by Cohen et al. showed flanker interference from contralesional distractors, and the magnitude of this effect was comparable to that observed for ipsilesional flankers. In terms of anatomy, two of the patients in that study (CR and PW) had lesions involving the TPJ, whereas the other patient (EH) had a lesion sparing

¹ Neglect patient PW was also tested with the same protocol as that used by Cohen et al. (1995). His overall data were consistent with those of the other two patients reported in their study, but were not included in that report.

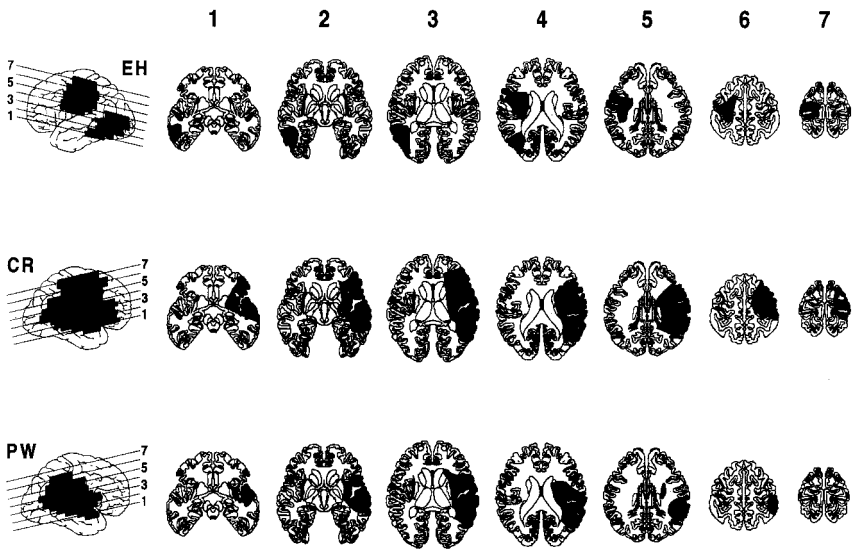


FIG. 4. The neuroimage reconstructions for the patients in the Cohen et al. (1995) study.¹

the superior temporal gyrus (see Fig. 4). Thus, only the data from patients CR and PW are at odds with the current findings.

However, there are two important methodological differences between the two studies. First, Cohen et al. tested their subjects over multiple sessions and obtained approximately 400 trials per session. In the current experiment, the patients were only tested in one session consisting of 96 trials. Second, the flanker and the target both remained on the screen until the subject responded in the Cohen et al. study; in the current study, the flanker was presented for less than 17 ms.

To assess the relevance of flanker exposure duration, one patient with a TPJ lesion (RS) was recruited for an additional test session. In this session, an unlimited flanker exposure (i.e., until a response was made) was used in one condition and a brief flanker exposure (17 ms) was used in another condition. The visual field by flanker congruency interaction was similar in both conditions: The congruency effect was larger in the ipsilesional hemifield compared to the contralesional hemifield in both the brief (53 ms vs. 34 ms) and unlimited (52 ms vs. 33 ms) flanker exposure conditions.

Since exposure duration was not critical, at least for this patient, he was tested in three more sessions of each task to determine if practice effects may account for the obtained differences between the current study and Cohen et al. Further testing of patient RS revealed an increase of the contralesional flanker effect over the course of testing (see Table 3). This observation suggested that the patients with TPJ lesions in the Cohen et al. study might have

TABLE 3

The Data from Patient RS in the Unlimited Flanker Exposure Conditions over the Course of Multiple Test Sessions

Patient	Session	Contralesional flanker		Ipsilesional flanker	
		Congruent	Incongruent	Congruent	Incongruent
RS	1	647	680	596	648
RS	2	553	650	646	715
RS	3	514	579	528	605
RS	4	516	561	542	595
EH	1	1845	2173	2229	1945
CR	1	945	1041	942	1097
PW	1	915	963	911	1114

Note. The congruent and incongruent conditions from the first session of the three neglect patients studied by Cohen et al. (1996) are also included for comparison.

initially shown an asymmetry in the first session of their study, but that this asymmetry was obscured when they averaged their data over multiple test sessions.

We reexamined the data of Cohen et al. to evaluate this prediction. The two patients with TPJ lesions initially showed larger ipsilesional flanker effects in their first session (see Table 3). Patient EH, whose lesion involved the inferior parietal lobule but spared the superior temporal gyrus, showed a larger contralesional flanker effect in the contralesional condition compared to the ipsilesional condition. Over the course of the multiple test sessions, the magnitude of the flanker effect increased in the contralesional condition for both patients whose lesion involved the TPJ. It remains to be determined why the influence of the flankers in the contralesional hemifield becomes greater over multiple test sessions. A recent study in patients with extinction also demonstrated that extinguished stimuli are detected with greater frequency over the course of testing (Kaplan, Cohen, Rosengart, Elsner, Hedges, and Caplan, 1995). It may be that processing is quite noisy in the lesioned hemisphere at the start of testing, but with practice, the results of this processing become manifest. Further testing is required to confirm this proposal.

We conclude from this investigation that attention or awareness of a distractor is not necessary to produce response channel activation. Converging behavioral evidence for the independence between spatial attention and flanker interference has also been obtained (Ro, Machado, Kanwisher, & Rafal, submitted for publication). The current results point to an important role of the temporoparietal junction in the activation of response channels. The dissociation between patients with lesions in this area compared to those in which the TPJ region was spared suggest that the anatomy, rather than

the syndrome of neglect, is critical in determining the impact on performance of information presented in the contralesional hemifield.

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