Distinguishing sensory and motor biases in parietal and frontal neglect

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Summary

Left neglect after right-hemisphere damage may involve perceptual and/or motor impairments. Here we discuss the limitations of previous attempts to separate these components, and introduce a new method. Six neglect patients (three with right inferior parietal lesions and three with right inferior frontal lesions) moved their right hand to a target light, which appeared unpredictably on either the left or the right of central fixation. The target appeared alone or with a distractor light in the opposite hemifield. Any directional motoric bias was measured by comparing reaches from a central start position with those for the same visual displays, but starting from the left of both possible targets (thus requiring only rightward reaches) or from the right (requiring only leftward reaches). All patients were slower to initiate reaches to left than right targets from a central start, which could reflect perceptual and/or motor biases. Critically, in the parietal neglect group only, initiation speed for left targets improved when a rightward reach was required to these (from a left start) rather than a leftward reach. This suggests a deficit in programming leftward movements into left hemispace, in addition to any visual impairment, for parietal neglect. A control task confirmed that this effect of start position was due to the associated change in reach direction and not to afferent inputs from the hand as it rested at the start position. Frontal neglect patients were slow to execute reaches to left targets, regardless of movement direction. Right visual distractors slowed visual reaction times to left targets more than vice versa in frontal neglect patients, and likewise for reach execution times in parietal neglect patients, suggesting that visual distractors on the neglected side have less impact. Distractor effects were unaffected by start position in the frontal neglect group (suggesting a perceptual basis), but distractors slowed reach initiation in the parietal neglect group only from left and central starts. Taken together, these findings demonstrate a directional motor component to parietal but not frontal neglect, and suggest that in man the inferior parietal lobe plays a role not only in perception but also in the programming of selective reaches. These conclusions are related to recent single-unit data from the monkey parietal lobe.

Keywords: attention; frontal lobe; motor control; neglect; parietal lobe

Abbreviations: ANOVA = analysis of variance; LED = light-emitting diode; RT = reaction time; TT = transport time

Introduction

Unilateral neglect is a relatively common outcome of unilateral brain damage in humans, especially after right-hemisphere stroke. Classically, the associated lesions involve the right inferior parietal lobe, but neglect may also occur in some form after lesions to other regions, including areas in the frontal lobe (Heilman and Valenstein, 1972; Mesulam, 1981; Vallar and Perani, 1986; Husain and Kennard, 1996). Neglect patients exhibit problems in judging or responding to information on the contralesional side of space. There is an emerging consensus that their difficulties reflect several

underlying impairments (Halligan and Marshall, 1992; Robertson and Marshall, 1993). Here we consider the influential view that perceptual and motor components of the syndrome may be dissociable (Heilman and Valenstein, 1979; Mesulam, 1985; Bisiach *et al.*, 1990). We consider motor biases arising for the intact ipsilesional limb, not the spontaneous underuse of the contralesional limb (Laplane and Degos, 1983; Mattingley and Driver, 1997).

Standard tests for left neglect (e.g. copying, cancellation and line bisection) do not distinguish between motor and

perceptual biases, because they typically require leftward responses (with the right hand) towards leftward visual information. Several new methods have been developed in an attempt to separate potential perceptual and motor components. Some studies have relied on spatial indices, such as the extent and accuracy of leftward versus rightward movements (e.g. Bisiach *et al.*, 1990), whereas others have used temporal indices, such as reaction time and transport time (e.g. Heilman *et al.*, 1985; for a full discussion, see Mattingley *et al.*, 1992).

Heilman and colleagues reported that right-hemisphere patients with left neglect were slower to initiate leftward than rightward movements when moving a handle along a track with their right hand (Heilman *et al.*,1985). While this is often considered a purely motoric deficit, perceptual deficits might also have been involved. Patients may have used vision to encode the desired end-point of the movement, this being impaired on the left. A similar ambiguity arises for subsequent studies, which similarly used temporal measures to document abnormal motor performance with the ipsilesional arm in neglect patients. Mattingley and colleagues found that left neglect patients were slower to initiate successive leftward than rightward movements with the right hand (patients with frontal and/or subcortical damage were also slow to execute these movements) (Mattingley *et al*., 1992). But since movements were cued visually in this study, the abnormal motor performance might have had some perceptual basis. The same problem of interpretation affects several other studies of motor performance under visual guidance in neglect (e.g. Goodale *et al.*, 1990; Harvey *et al.*, 1994; Mattingley *et al.*, 1994).

In an effort to overcome such interpretative difficulties, several studies set perceptual and motor demands in spatial opposition. These studies involved spatial rather than temporal measures of performance. Coslett and colleagues occluded direct vision of the hand during line bisection, providing visual feedback via a video image that could appear in the same or opposite hemispace (Coslett *et al.*, 1990). However, placing video feedback on the opposite side not only dissociates the hemispace of motor response from that seen visually; it also sets the side of kinaesthetic inputs (from the responding hand) against the side of visual feedback. Thus, any difference between feedback in the same versus opposite hemispace might conceivably be due to a difference in the severity of neglect for visual versus kinaesthetic inputs (Vallar *et al.*, 1993) rather than to perceptual versus motor dissociation. Note also that the direction of hand movements, and of visual scanning, was unconstrained in the study of Coslett and colleagues.

Subsequent studies devised related techniques specifically to oppose the direction of motor and visual responses, across both hemispaces. Tegnér and Levander (Tegnér and Levander, 1991) placed a pair of mirrors, abutting at 90°, behind Albert's line-cancellation test (Albert, 1973), so that hand movements during cancellation appeared to traverse the page in the opposite direction when viewed in the mirror. On

standard cancellation (i.e. with direct visual feedback from the responding hand), neglect patients failed to cancel targets towards the left of the page. In the mirror-reversed ('incompatible') condition, most patients moved their hand leftwards across the page until it was reflected on the right side of the mirror, then proceeded to cancel from there, with omissions arising on the right side of the page (now seen on the left). Some patients, however, failed to move their hand across to the left side of the page for the incompatible condition. These latter patients, whose extensive lesions typically extended into the frontal lobe, were considered to have a motor rather than a perceptual form of neglect, failing to make hand movements in the contralesional direction for both standard and incompatible conditions. Using the same reversing-mirror method, Bisiach and colleagues found that the pattern shown by some right-hemisphere patients could change (i.e. from the apparently perceptual outcome to the 'motor' result, or vice versa) depending on where the responding hand was positioned at the start of each trial (Bisiach *et al.*, 1995). This casts doubt on any claim that perceptual versus motor neglect, as revealed by the mirror task, is an immutable diagnosis.

There are a number of potential difficulties in interpreting data from the mirror opposition technique. First, cancellation via a reversing mirror is extremely incompatible even for healthy subjects. Patients might fail the task because of general non-spatial problems with incompatible tasks, which may lead some to give up in the mirror-reversed condition after just a few initial attempts to cancel items near where their hand starts. This alone could lead to an apparently motor pattern of deficit when the start position is on the right (the default position for the right hand). It could also explain the change from apparently motor to apparently perceptual neglect which Bisiach and colleagues found between trials when the start position was varied (Bisiach *et al.*, 1995).

Our suggestion that the supposedly motor pattern in mirror cancellation might be due to patients giving up in the incompatible condition seems consistent with the anterior lesions associated with this pattern (Tegnér and Levander, 1991; Bisiach *et al.*, 1995). Large frontal lesions are well known to produce difficulties with highly incompatible tasks (e.g. Duncan, 1995). Thus the supposedly motor frontal pattern of responding in the mirror task might be due to general deficits for incompatible tasks rather than to directional motor neglect. In a recent PET study, Fink and colleagues showed that right dorsolateral frontal cortex is activated in normal subjects when a mirror provides spatially reversed visual feedback during control of hand movements (Fink *et al.*, 1999). This is consistent with our suggestion that frontal structures may be particularly susceptible to the incompatibility of mirror-reversing tasks.

A further technique for separating perceptual and motoric factors was introduced by Mijović (Mijović, 1991). Neglect patients searched for a visual target in a display that was hidden beneath a mask containing a small viewing window. In one condition, patients moved the mask until the target

appeared beneath the window (so leftward movements revealed leftward targets), and in another they moved the target display under the stationary mask (here rightward movements reveal leftward targets). Patients were slow to find targets on the contralesional side of the display in both conditions, suggesting that perceptual rather than motoric biases dominated in this task. However, the perceptual factors of this task are arguably more demanding than the motor component, since the visual layout of the display must be reconstructed from successive fragments appearing beneath the window.

One feature of all of the opposition methods discussed so far is that they are rather unconstrained; the patient is free to direct hand (and/or eye) movements in any direction in order to cancel or identify targets. The pulley opposition method devised by Bisiach and colleagues allows greater control over the direction of patients' hand movements (Bisiach *et al.*, 1990). In this variant of line bisection, patients moved a pointer leftwards or rightwards via a pulley to indicate the apparent midpoint of a line. In the compatible condition, patients moved the pointer directly; in the incompatible condition they operated the pulley such that leftward hand movements shifted the pointer right, and vice versa. Right-hemisphere patients bisected lines to the right of the true midpoint in the compatible condition, as expected for left neglect. In the incompatible condition, some patients bisected as before, others now bisected further to the left, and some even made paradoxical errors to the left of the true midline. Changes in performance between compatible and incompatible conditions were again observed predominantly in patients whose extensive lesions included frontal regions, and it was suggested that such damage produces a motor form of neglect. Once again, however, the novel version of the task is highly incompatible, and this alone might account for its sensitivity to frontal lesions.

In summary, it is now well established that many neglect patients exhibit abnormalities in motor performance with the non-paretic ipsilesional arm. But the cause of these abnormalities remains unclear, and attempts to separate perceptual and motor impairments with opposition methods suffer from introducing incompatibility to the task. The goal of the present study was to develop a new method which might separate visual and motoric components of neglect less ambiguously, in a manner allowing both to be measured at the same time, and within a natural reaching task that does not introduce any substantial incompatibility.

The paradigm we devised was based on temporal measures in a selective reaching task (Tipper *et al.*, 1992, 1997; Howard and Tipper, 1997). In this paradigm, subjects reach to visual targets while the presence of concurrent visual distractors is manipulated. A recent study (Behrmann and Meegan, 1998) adapted this basic paradigm for neglect patients and found that, whereas distractors on the ipsilesional side of targets can produce interference with reaches, those on the contralesional (neglected) side produce little or no interference. However, as with the many results reviewed

earlier, it remains uncertain whether this biased interference pattern in neglect patients reflects perceptual or motor factors, or some combination.

Here we introduce a new manipulation that may allow the separation of perceptual and motor components while also examining distractor effects. We examined these aspects of neglect in patients with focal lesions of either the right inferior parietal lobe or the right frontal lobe. In this way, we could assess previous claims that frontal damage may have a special association with directional motor impairment in the neglect syndrome (Bisiach *et al.*, 1990, 1995; Tegnér and Levander, 1991; Mattingley *et al.*, 1992). Note that, to date, such claims have been based not on patients with focal frontal lesions but rather on patients whose large lesions extended across both the frontal and the parietal lobe in the right hemisphere. Some of the initiation-time results of this study have appeared in preliminary form in a short letter (Mattingley *et al.*, 1998*b*).

Experiment 1

Patients were first required on each trial to fixate a central yellow light-emitting diode (LED), aligned with the body midline. A green target LED could then be illuminated transiently in either the contralesional or the ipsilesional hemispace, at a fixed eccentricity (Fig. 1). The patients' reaching task was to move their ipsilesional hand as rapidly as possible from a start-key, to press a button immediately below the green target. This target could occur alone, or with a red distractor LED illuminated simultaneously in the opposite hemispace. Interference from distractors was measured by comparing performance for target-only trials against the same green target in the presence of a red distractor. To discourage anticipatory responses, occasional catch trials were included where only a red distractor LED was illuminated, and the patient was required to withhold movement.

From a central start position (Fig. 1A), left neglect patients would be expected to show poorer performance when reaching to a left rather than to a right target. As regards the underlying impairment, such a left-sided disadvantage in motor performance would have the same ambiguity as conventional tests for neglect; it would be unclear where along the sensory–motor continuum the spatial bias arose. Slow responses to left targets might be due to difficulties with perception for that side, or to deficits in motor programming and/or execution for that side, or even to some combination of these. Rather than set perceptual and motor factors in opposition, we simply varied the start position of the ipsilesional hand, for a reach that in all other respects remained natural.

When the start key is located centrally, a left target requires a leftward movement. By contrast, when the start key is shifted to the left side of both targets (Fig. 1B), even a target in the left visual hemifield now requires a rightward reach. Thus, if neglect for left targets from a central start involves problems in programming or executing leftward movements,
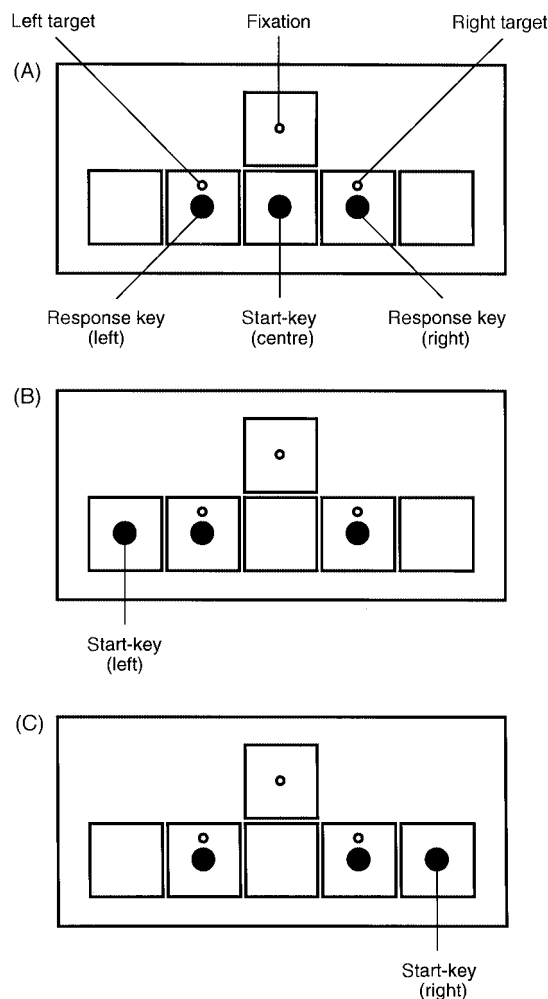
Fig. 1 Apparatus used for distinguishing sensory and motoric biases in neglect. In the reaching task (Experiment 1) patients moved their ipsilesional hand from the start key to press a response key beneath the target LED. In the press-at-start task (Experiment 2) patients pressed the start key when they detected the target LED. (**A**) Centre-start position; (**B**) left-start position; (**C**) right-start position.

Fig. 2 Lesion reconstructions plotted on standard templates (Damasio and Damasio, 1989): (**A**) parietal neglect patients; (**B**) frontal neglect patients.

then performance for the same targets should improve significantly from a left start. If any left neglect is due instead to purely visual biases, then the change in start position should presumably have no effect, since with central fixation the locations of visual target and distractor events remain unchanged. For completeness, we also included a condition in which the start key was located to the right of both possible target loci (Fig. 1C). In this condition, targets in both left and right hemifields require leftward movements to reach them.

Method
Patients
We initially screened a large number of right-hemisphere patients exhibiting visuospatial neglect. We then tested in detail only those with circumscribed lesions which could be
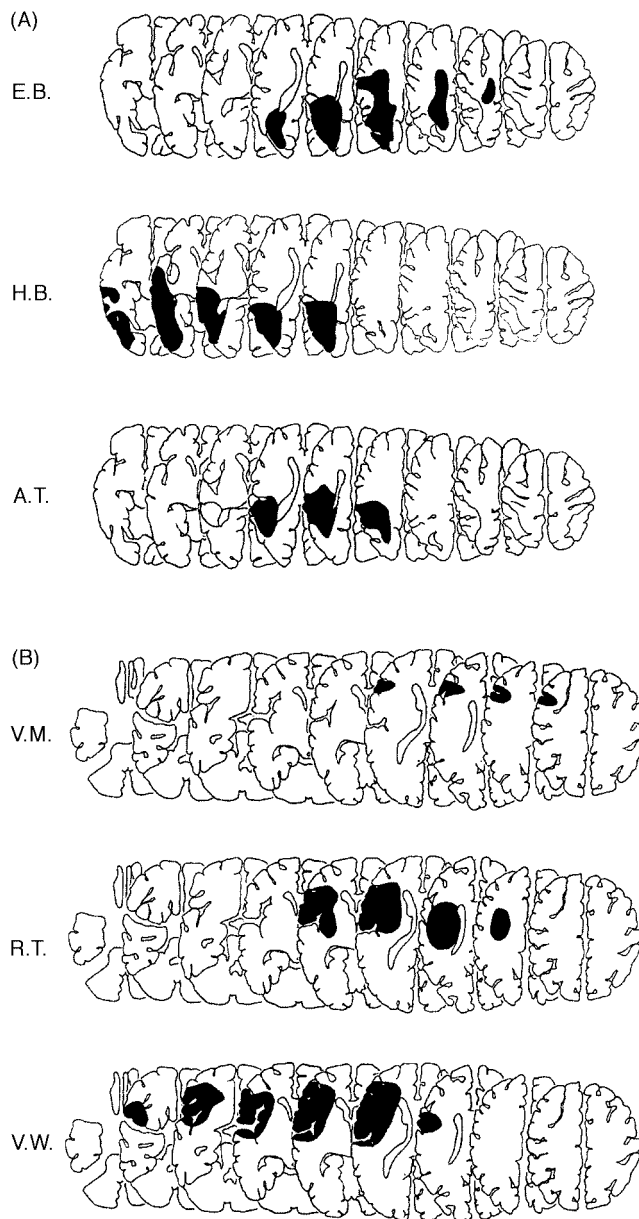
localized, on the basis of structural neuroimaging, to either the frontal cortex sparing the posterior parietal lobe ($n = 3$) or to predominantly the posterior parietal cortex sparing the frontal lobe ($n = 3$). These six stroke patients with discrete right-hemisphere lesions, and with left visuospatial neglect on conventional tests, served as the experimental subjects. Brain lesions were imaged by cranial CT or MRI and mapped by hand onto standard axial templates (Damasio and Damasio, 1989) (Fig. 2). Three patients had damage centred on the inferior parietal lobe, with sparing of the frontal lobe (Fig. 2A), and three had damage to the frontal lobe, with sparing of the posterior parietal lobe (Fig. 2B). All patients were right-handed and all had full visual fields on clinical confrontation

Table 1 *Clinical details and test performances of patients with left unilateral neglect*

Patient	Age (years)	Sex	Interval after stroke (days)	Mesulam cancellation (/60)	Line bisection (BIT score)
(A) Parietal neglect					
E.B.	81	F	6	52	6
H.B.	75	F	24	12	1
A.T.	59	M	64	34	5
Mean (SD)	71.7 (11.4)		31.3 (29.7)	32.7 (20.0)	4.0 (2.7)
(B) Frontal neglect					
V.M.	61	F	59	36	8
R.T.	61	M	77	34	6
V.W.	78	F	61	32	9
Mean (SD)	66.7 (9.8)		65.7 (9.9)	34.0 (2.0)	7.7 (1.5)

BIT = behavioural inattention test.

testing. None had bilateral damage, dementia, previous neurological illnesses or gaze palsy. Personal and clinical details for each patient are provided in Table 1.

In addition to our lesion criteria, patients were selected for inclusion only if they were impaired on Mesulam's shape-cancellation test (Mesulam, 1985) (see scores in Table 1A and B). The line bisection task from the Behavioural Inattention Test (Wilson *et al.*, 1987) was also administered. Both tests followed the standardized procedures. As groups, our parietal and frontal patients were comparable in terms of age and severity of clinical neglect (cf. data in parts A and B, Table 1). Four neurologically healthy control subjects were also tested [mean age 67.8 (13.3) years]. All subjects gave informed written consent before testing for both experiments. The study was approved by the ethics committee of Charing Cross Hospital.

Apparatus

A Perspex board (594 × 282 mm) on which were mounted six white plastic boxes (100 × 100 × 45 mm) was placed on a table surface (Fig. 1). One box, mounted centrally towards the distal edge of the board, had a yellow LED at the centre of its top surface, which served as the fixation point at the beginning of every trial. Three other boxes were each fitted with a microswitch at their centre, with a circular black disk (32 mm in diameter) on top of it serving as a button which subjects might have to depress with their right index finger. Two of these boxes were also fitted with a red/green bicolour LED located 5 mm above the response key. These bicolour LEDs provided potential target or distractor stimuli. The third box with a microswitch (but no LED) served as the start key on which the subject's index finger rested before the initiation of each trial. This start box was attached to the Perspex board by means of Velcro strips, so that it could be moved from its central position between the two boxes containing target/distractor LEDs (as in the arrangement shown in Fig. 1A), to the alternative start positions either on the extreme left or right of the target/distractor boxes (Fig. 1B and C). The remaining two boxes

contained neither microswitches nor LEDs and were used simply to fill the two empty spaces that remained in the row of five when the start box was moved from one of its three positions (extreme left, centre, and extreme right) to another. All aspects of stimulus control and response recording were handled by a laptop computer which interfaced with the microswitches and LEDs.

Procedure

Subjects sat with their midsagittal axis aligned with the central fixation LED. All responses were made with the extended index finger of the right hand. All trials began with the yellow fixation light being illuminated at the centre of the apparatus. This was the signal for subjects to place their right hand on the start key and hold it down. An examiner sitting opposite the patient checked to ensure correct central fixation of the yellow LED before the beginning of every trial, and subjects were verbally reminded of this fixation requirement whenever necessary. At a variable interval (500–1000 ms) after depression of the start key, the fixation light was turned off and simultaneously either one or two of the peripheral bicolour LEDs were illuminated, ~8° from fixation. On target-only trials, one LED turned green. On target-plus-distractor trials, the LED on the other side was illuminated in red simultaneously with the green target. On catch trials, only one LED was illuminated, in red.

Subjects were asked to reach as quickly as possible to press the key beneath a green LED and to ignore any red LED. They were instructed not to move from the start key on catch trials with only a red LED. Target and distractor LEDs remained illuminated until a response key was pressed, or for a maximum of 4000 ms. After an intertrial interval of 1600 ms, the yellow fixation LED was illuminated once more and the subjects were instructed to bring their hand back to the start key (if a movement had been made) in preparation for the next trial. They were also reminded to fixate the central yellow LED.

The computer recorded (i) subjects' reaction times (RTs) to initiate movements away from the start key in milliseconds;

(ii) movement transport time (TT), from releasing the start key until a further key was depressed; and (iii) any errors (i.e. failures to respond within 4000 ms, responses on catch trials or presses of inappropriate keys). Our analyses focus primarily on RT rather than TT, as the amplitude of some of the required reaches varied as a function of start position (with a central start, the left and right targets required reaches of similar amplitude, but with a left start the right targets required a reach that was twice as long as for left targets, and vice versa for a right start) (Fig. 1). When TT is considered, we focus on any differences between reaches of similar amplitude as a function of start position.

Each patient completed a minimum of two blocks of trials at each start position (left, centre, right) in an ABCCBA design. Normal controls completed four blocks of trials at each start position in a similarly counterbalanced manner. There were 50 trials per block, comprising 20 target-only (10 left, 10 right), 20 target-plus-distractor (10 target-left, 10 target-right) and 10 catch trials (five distractor-left, five distractor-right), all in a randomly intermingled order within each block. The sequence of blocks with different start positions (left, centre or right) was randomized across subjects. Moreover, blocks of trials from the control task of Experiment 2 (described later) were intermingled with blocks from the reaching task of Experiment 1, to allow a comparison of the two tasks that was not confounded with any session effects. (The two experiments were actually run together, and are presented separately here only for ease of exposition.) Before experimental blocks, each subject completed a minimum of 15 practice trials. Patients A.T., E.B. and V.W. sometimes failed to respond to contralesional targets altogether, so they completed six further experimental blocks of trials in addition (making 12 blocks in total across the two experiments, four at each start position) to increase the number of trials available for statistical analysis.

Results and discussion

Our initial analyses tested any RT difference for reaches to left and right targets from a central start. A disadvantage for left targets was expected given the diagnosis of left neglect in clinical tests (Table 1), regardless of whether this neglect was due to perceptual biases, motor biases, or some combination. Independent-samples *t*-tests were conducted separately for each patient, entering every trial as an observation and comparing correct RTs to left and right targets (collapsed across target-only and target-plus-distractor trials) from the central start. All patients were slower on average to initiate movements to left versus right targets (Fig. 3). The *a priori* prediction of slower RTs to left versus right targets was reliable individually for all patients ($P <$ 0.05) except R.T. (Fig. 3).

Analyses of RTs

Repeated-measures analyses of variance (ANOVAs) on mean correct RTs for the parietal, frontal and control subjects
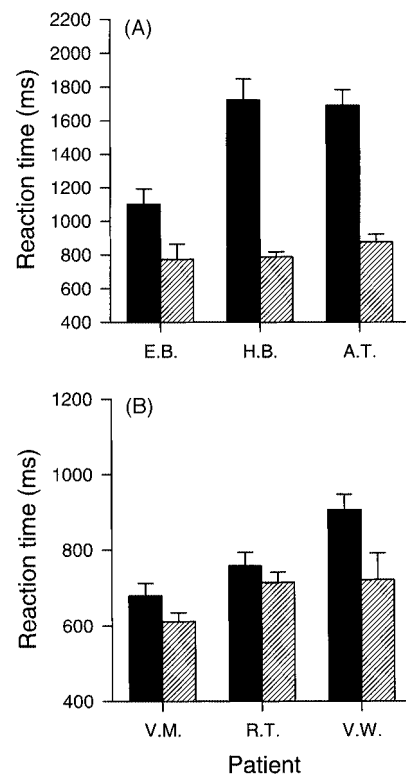

Fig. 3 Mean reaction times (with 1 SE indicated) for correct reaches to targets from centre-start position (pooled across target-only and target-plus-distractor trials), plotted separately for each patient (**A**, parietal neglect patients; **B**, frontal neglect patients). Solid and hatched bars represent reaches to left- and right-sided targets, respectively. Note the different vertical scales.

(initially analysing these three groups separately) had the factors of Start Position (left, centre, right), Target Side (left, right) and Distractor Condition (target-only, versus target-plus-distractor). Errors and false alarms are reported separately below. For ease of exposition, we consider the influences of hand Start Position and Target Side first.

Influence of hand start position and target side on RTs

The mean correct RT data for left and right targets, plotted with separate lines for left, central and right start positions, are shown for each group in Fig. 4A–C, collapsed across Distractor Condition.

For parietal neglect patients, there was a main effect of Start Position [$F(2,4) = 7.9$, $P < 0.05$], in addition to a marginal effect of Target Side [$F(1,2) = 11.9$, $P < 0.08$]. More importantly, there was a reliable two-way interaction between Start Position and Target Side [$F(2,4) = 6.8$, $P = 0.05$]. This critical result arose because the substantial disadvantage in RT for left versus right targets with central and right start positions was greatly reduced with a left start position, exactly as predicted if moving rightwards to a left visual field target reduces the neglect for it (Fig. 4A).
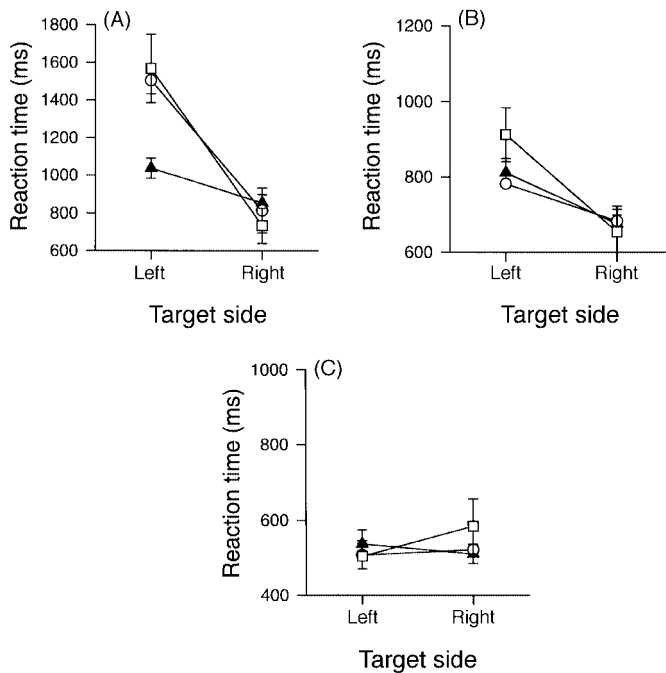
Fig. 4 Mean reaction times (±1 SE) for correct reaches to left- and right-sided targets (pooled across target-only and target-plus-distractor trials) plotted as a function of start position. Solid triangles, open circles and open squares represent data from left-, centre- and right-start positions, respectively. (**A**) Parietal neglect patients; (**B**) frontal neglect patients; (**C**) healthy controls. Note the different vertical scales.

The three-way interaction involving the additional factor of Distractor Condition did not approach significance [$F(2,4) = 0.4$, n.s.], so the critical modulation of left neglect by hand start position in the parietal group (Fig. 4A) was unaffected by distractors. The reduced left neglect with a left start position was confirmed in separate planned comparisons, using the Bonferroni correction. RTs were slower for left than right targets from a central start [$F(1) = 27.7$, $P < 0.01$, mean difference 692 ms], and likewise from a right start [$F(1) = 40.4$, $P < 0.01$, mean difference 834 ms]. By contrast, there was no reliable RT difference between left and right targets from a left start [$F(1) = 1.9$, n.s.].

In contrast to these findings for parietal neglect patients, the frontal neglect patients did not exhibit any reliable modulation of neglect by Start Position in their RT data. Neither the two-way interaction of Start Position with Target Side [$F(2,4) = 2.9$, n.s.] nor the three-way interaction of Start Position with Target Side with Distractor Condition [$F(2,4) = 0.8$, n.s.] approached significance. As Fig. 4B shows, unlike the parietal neglect patients (cf. Fig. 4A), the RT cost for reaching to left versus right targets was similar across the three start positions in the frontal neglect patients, and in particular was equivalent for the centre and left starts, which differed so markedly for the parietal neglect group. This null effect of start position applied for the frontal neglect patients regardless of whether a simultaneous distractor was present, and indeed the Start Position factor was not involved

in any significant term for this group. An ANOVA conducted on RTs for controls also failed to reveal any significant main effects or interaction, as expected for this neurologically intact group of subjects (Fig. 4C).

To verify that the influence of start position on the severity of neglect (i.e. on the RT disadvantage for left targets) did indeed differ between groups (as our separate analyses for each group suggest), a further ANOVA was performed on all three groups together, with the added between-subjects factor of Group (parietal, frontal, control). This mixed ANOVA revealed a main effect of Group [$F(2,7) = 10.4$, $P < 0.01$], with parietal and frontal patients unsurprisingly showing slower overall RT (mean 1085 and 753 ms, respectively) than controls (mean 528 ms). Critically, there were several two-way interactions, all subsets of the crucial three-way interaction between Group, Start Position and Target Side [$F(4,14) = 7.6$, $P < 0.01$]. This significant interaction confirms within a single analysis that the difference in RTs for left versus right targets was indeed affected differently by start position in parietal neglect patients, versus frontal neglect patients and controls, consistent with the within-group analyses presented above (cf. part A with parts B and C in Fig. 4).

Can the critical effect of hand start position on the extent of left neglect in RT for the parietal group also be demonstrated within each parietal patient as an individual? Mean RTs are shown separately for each of the three parietal patients in Fig. 5 (again pooled across the factor of Distractor Condition, which did not affect the critical result). All three patients showed a smaller RT cost for left versus right targets from a left start position than from the central and right start positions (compare the lines with filled triangles in each plot of Fig. 5 with the lines with open circles and squares). Using separate ANOVAs on each patient, with each trial entered as an observation, the two-way interaction between Start Position and Target Side reached significance within two of the three patients [patient H.B., $F(2,130) = 6.7$, $P < 0.01$; patient A.T., $F(2,130) = 8.6$, $P < 0.001$]. In patient A.T., t-tests showed significantly slower RTs [$t(58) = 4.3$, $P < 0.001$] for left than for right targets from a right start, and likewise from a central start [$t(56) = 5.6$, $P < 0.001$], but no such neglect from a left start [$t(65) = 0.3$, n.s.]. H.B. showed a similar pattern of stronger left neglect from right [$t(29) = 5.5$, $P < 0.001$] and central starts [$t(33) = 6.4$, $P < 0.001$] than from left starts, although he still showed some neglect in the last case [$t(68) = 2.0$, $P < 0.05$]. Finally, although the two-way interaction did not reach significance within E.B. when analysed alone, she too showed stronger neglect from right [$t(70) = 4.0$, $P < 0.001$] and central starts [$t(67) = 2.2$, $P < 0.05$] than from left starts [$t(75) = 1.2$, n.s.]. Thus, the pattern of less neglect from a left start was present within each patient as an individual. In contrast, none of the three frontal patients showed the critical outcome of a reduced difference between RTs to left and right targets when the hand started from the left.
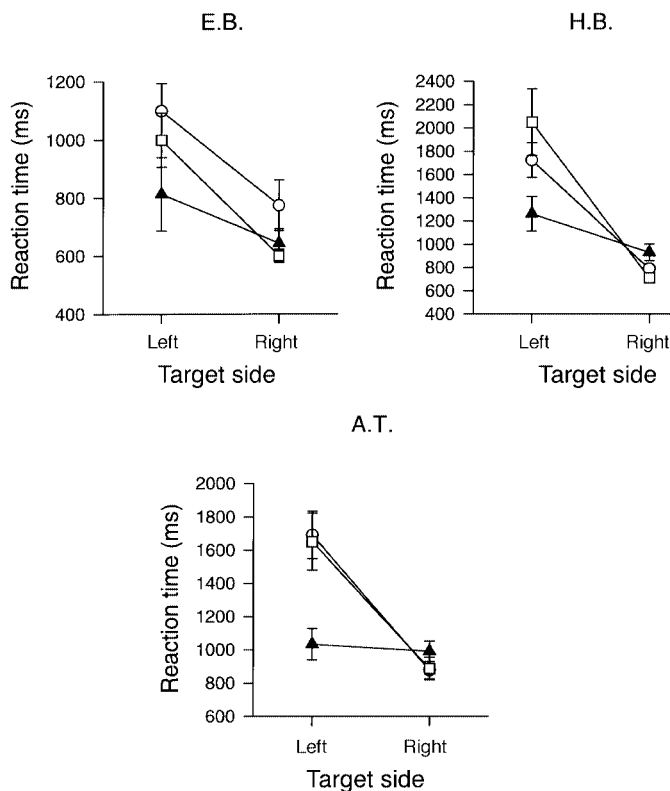
E.B.

H.B.

A.T.

Fig. 5 Mean reaction times (±1 SE) for correct reaches to left- and right-sided targets (pooled across target-only and target-plus-distractor trials), plotted on separate axes for the three parietal neglect patients (E.B., H.B. and A.T.). Solid triangles, open circles and open squares represent data from left-, centre- and right-start positions, respectively. Note the different vertical scales.

Influence of distractors on RTs

In our preliminary analysis of RT data from the two patient groups (Mattingley *et al*., 1998*b*) we pooled over target-only and target-plus-distractor trials, as this factor did not modify the crucial effect of start position on reach RTs to left versus right targets in parietal patients, nor was the absence of this interaction in the frontal group affected by distractors (as discussed above). Here we report the full results of the RT analysis on data from both patients and healthy controls, with Distractor Condition included.

The repeated-measures ANOVAs on correct RTs, conducted separately for the parietal, frontal and control groups (with the factors of Start Position, Target Side and Distractor Condition), revealed a trend for frontal patients to be slower at initiating movements in target-plus-distractor trials (774 ms) than target-only trials (732 ms) [$F_{(1,2)} = 10.4$, $P = 0.08$], regardless of Start Position or Target Side. The only fully significant influence of Distractor Condition was in the parietal group, where there was a significant two-way interaction between Start Position and Distractor Condition [$F_{(2,4)} = 10.2$, $P < 0.05$]. Separate one-way ANOVAs on data from each Start Position alone (with the single factor of Distractor Condition) failed to reveal significant effects, because of insufficient power. Never-

theless, the significant two-way interaction in the parietal data indicates that the distractor effects were largest for the left start position (mean interference effect of 161 ms), somewhat less pronounced for the central start position (68 ms interference) and negligible for the right start position (a mean of 18 ms faster with a distractor).

Thus, the only important effect of distractors on RTs appears to be restricted to the parietal group. For these patients, distractors interfere with reach initiation only when the hand starts from the left or centre start positions, not when it starts from the right (where, if anything, distractors now speed rather than slow RTs). Note that the visual location of the distractor (which was always opposite the target side) is not critical here, only the start position of the hand. This again suggests that the direction of reach may be an important factor, for the parietal patients in particular. When the hand starts from the right and must always reach leftwards, any cost from a distractor is evidently outweighed, for the parietal left-neglect patients, by a benefit from having two concurrent visual events (target plus distractor) signalling that the patient should initiate a leftward movement. One possible interpretation is that since right-parietal patients encounter difficulties in reaching leftwards, two simultaneous visual events (target plus distractor), both in the same direction from the hand, are more helpful than one event (target alone) in triggering this otherwise problematic leftward movement.

As mentioned previously, a mixed ANOVA on RTs was also performed for all three groups together, with the additional between-subjects factor of Group (parietal, frontal, control). In addition to the terms mentioned in the previous section, there were some reliable terms involving Distractor Condition: two-way interactions between Group and Distractor Condition [$F_{(2,7)} = 4.8$, $P < 0.05$] or between Start Position and Distractor Condition [$F_{(2,14)} = 3.7$, $P = 0.05$], both as subsets of the three-way interaction of Group × Start Position × Distractor Condition [$F_{(4,14)} = 2.9$, $P < 0.06$]. This confirms within a single analysis the pattern described above: an influence of distractors which depends critically upon hand start position (i.e. no distractor cost from a right start only) and is specific to the parietal group.

Analyses of TTs

The mean correct TT data for left and right targets are shown in Table 2 as a function of Start Position and Distractor Condition, separately for parietals, frontals and controls. A mixed ANOVA was performed with the between-subjects factor of Group (parietal, frontal, control) and within-subjects factors of Start Position, Target Side and Distractor Condition. There was a significant main effect of start position [$F_{(2,14)} = 5.7$, $P < 0.05$], with TTs from left and right start positions (464 and 448 ms, respectively) being significantly longer overall than TTs from a central start (355 ms). This may arise simply because reaches from the extreme left and right start positions were on average larger in amplitude than reaches from the central start position (Fig. 1). Accordingly,

Table 2 *Mean (standard error) transport times in milliseconds for correct reaches made by parietal and frontal neglect patients and healthy controls as a function of Start Position, Target Side and Distractor Condition*

Start Position:	Hand left				Hand centre				Hand right			
Target Side:	Left		Right		Left		Right		Left		Right	
Distractor Condition:	T	T+D	T	T+D	T	T+D	T	T+D	T	T+D	T	T+D
Parietal neglect patients	589 (230)	587 (225)	680 (194)	635 (182)	438 (107)	581 (147)	417 (110)	408 (86)	649 (156)	826 (216)	351 (86)	444 (142)
Frontal neglect patients	454 (118)	475 (106)	665 (136)	646 (129)	454 (61)	475 (63)	383 (65)	413 (94)	670 (72)	662 (99)	418 (52)	443 (37)
Control subjects	211 (34)	207 (30)	334 (35)	337 (38)	246 (32)	246 (30)	191 (11)	187 (19)	360 (48)	356 (45)	206 (26)	205 (33)

T = target only; T+D = target + distractor.

any influences of start position on TT are considered below only for reaches of comparable amplitude.

There was a significant main effect of Target Side [$F(1,7)$ = 11.5, $P < 0.05$], with longer TTs for left versus right targets overall and of Distractor Condition [$F(1,7) = 5.9$, $P < 0.05$], TTs being significantly longer for targets with a simultaneous distractor (432 ms) than for targets alone (412 ms). More importantly, there was a three-way interaction between Group, Target Side and Distractor Condition [$F(2,7) = 4.6$, $P = 0.05$]. When broken down into separate two-way ANOVAs on TTs for left and right targets (with factors of Group and Distractor Condition), there were no significant effects in the ANOVA on right-target data, but a nearly significant interaction in the left-target data between Group and Distractor Condition [$F(2,7) = 4.2$, $P = 0.06$]. For the parietal neglect patients, TTs to left targets were 106 ms slower when there was a (right) distractor, whereas TTs to right targets were only 12 ms slower when there was a (left) distractor. This asymmetrical distractor effect was absent for the controls (3 versus 1 ms for left and right targets, respectively) and for the frontal neglect patients (11 versus 13 ms for left and right targets, respectively). Thus, for right parietal neglect patients only, ipsilesional distractors interfered with TT more than contralesional distactors (reminiscent of the pattern observed by Behrmann and Meegan, 1998). The frontal neglect patients and control subjects showed no reliable influences of distractors on TT and thus no asymmetry between ipsilesional and contralesional distractors (Table 2).

In separate repeated-measures ANOVAs conducted on TT for each group, Distractor Condition did not interact with Start Position, even for the parietal neglect group, which showed the asymmetrical distractor effects. The greater influence of an ipsilesional distractor compared with a contralesional distractor on TTs in the parietal group therefore need not have a motor origin; it may instead be due to a purely perceptual component of their neglect [a point which also applies to Behrmann and Meegan's distractor-interference results (Behrmann and Meegan, 1998)]. That is, unlike the overall pattern in reaching RTs described earlier for this group (Figs 4A and 5), distractor interference on TT did not vary with start position and the consequent change in reach direction.

To assess whether start position had any influence on overall TT to a given target for the parietal patients (as found for their RTs to left targets) when movement amplitude was held constant across the different start positions, we conducted several planned comparisons. These concerned parietal mean TTs for left targets (pooled over Distractor Condition) from left versus central start positions (mean 588 and 510 ms, respectively) and for right targets from central versus right start positions (mean 413 and 397 ms) in the parietal group. Note that each of these comparisons involves the execution of reaches to the same target with a constant amplitude but in opposite directions. Neither comparison was significant, showing that the TT measure in this group did not differ

reliably between different start positions, not even for reaches of similar amplitude but opposite direction towards the same left target.

For the frontal neglect group, a repeated-measures ANOVA on TT revealed a main effect of Target Side [$F(1,2) = 26.8$, $P < 0.05$], with slower reach execution overall to left (532 ms) than right targets (495 ms). Thus, regardless of the direction of the reach, execution of movements to left targets was significantly slower overall than for right targets in the frontal neglect patients. However, some caution is required in attributing this to a specific frontal impairment, as a similar (non-significant) trend was apparent in the other groups, and the interaction between Group and Target Side did not reach significance in the mixed ANOVA on TT described earlier. Planned comparisons to assess effects of reach direction for movements of constant amplitude found no differences between mean TTs for left targets from left and central start positions (mean 465 ms for both conditions), or for right targets from central versus right starts (mean 398 and 431 ms, respectively), in the frontal neglect patients.

Errors and false alarms

Errors (i.e. failures to respond within the 4 s deadline, or presses of incorrect keys) and false-alarm responses (i.e. movements on catch trials) are tabulated separately for parietal and frontal neglect patients in Appendix A as a function of Start Position and Target Side. For the two patient groups, false alarms occurred only rarely, and no terms were significant in repeated-measures ANOVAs for the parietal and frontal neglect groups. Errors were somewhat more common with left than with right targets (Appendix A), consistent with the patients' neglect, but no terms reached significance in repeated-measures ANOVAs on this measure for either group. Unsurprisingly, normal controls made very few errors or false alarms (just 28 in total from 2400 trials), too few for statistical analysis.

Conclusions from Experiment 1

Patients with damage centred on the right inferior parietal lobe all showed modulation of their left neglect by hand-start position, implying some motor component of their deficit for left targets, in addition to their clear visual deficit. For all three parietal neglect patients, the substantial RT disadvantage for left targets was reduced when the hand started from the left, so that only rightward movements were now required (Figs 4A and 5). Since the visual target events were identical regardless of start position, and central fixation was required and monitored, this suggests that some component of the parietal neglect patients' difficulty with left targets from a central start position is due to a problem in planning and initiating leftward movements into left hemispace.

When reaches were made from the right start position, RTs to left and right targets were not significantly different from those observed from the centre start position in the parietal neglect group. Thus, reaches to left targets still took longer to initiate than those to right targets, even though both movements were now leftward. This implies that the impairment in movement initiation for the parietal neglect patients is not simply a disorder of directing any movement in a leftward direction, but is specific to movements made in a leftward direction to targets in left hemispace.

The effect of start position on reaching RT for the patients with parietal neglect was not apparent in the frontal neglect patients (Fig. 4B), collectively or as individuals, nor was it apparent for normal controls. This difference between groups demonstrates that the influence of start position found in the parietal neglect group cannot be some peculiar artefact intrinsic to our method, because the parietal pattern of results was not found invariably. Moreover, the start position effect cannot be merely a consequence of larger lesions in the parietal neglect group; it was significant in all three parietal patients as individuals despite the different extent of their damage (Fig. 5), and it was absent in the frontal neglect patients with similar lesion volumes.

Analysis of TT data did demonstrate that, once initiated, the reaches of frontal neglect patients were significantly slower to left targets than to right targets, regardless of the direction of the reach. This might suggest a motor impairment in the execution of reaches to targets in left hemispace, regardless of the start location. Such a deficit would be consistent with the original suggestion by Mattingley and colleagues that the execution phase of movement is selectively disrupted after anterior lesions (Mattingley *et al.*, 1992). However, in that study the impairment of movement execution in patients with anterior lesions was determined by the direction of reach (so-called directional bradykinesia) rather than by the hemispace in which the target occurred, as in the present study.

The presence of distractors exerted several influences, delaying both RT and TT overall (consistent with the normal studies of Tipper *et al.*, 1992, 1997). Two distractor effects were specific to the parietal group. First, in the RT measure, distractors interfered only when reaching from the left and centre starts in these patients, not from a right start (where, if anything, the distractor actually speeded responses). This might be due to the additional visual stimulation helping the parietal neglect patients to initiate the leftward movement that is problematic for them. Secondly, in the TT measure, right distractors interfered with reaches to left targets, but not vice versa. Since this particular parietal result was not modulated by start position, it might be due to a purely visual component of these patients' deficit.

Experiment 2

In the above discussion, we assumed that the influence of start position on parietal neglect in the RT measure was due to the direction of reach required for a target in left hemispace (which changed from leftward to rightward when a left start

was used). Could start position instead have affected the degree of neglect via some form of cueing by afferent inputs from the responding hand, as it waited at the start position before each trial commenced? Tactile and/or proprioceptive inputs from the hand might somehow have biased covert visual attention towards it, thus leading to less left neglect with a left-start position (Halligan *et al.*, 1991; Mattingley *et al.*, 1993). If so, the results of Experiment 1 would still reveal an important difference between our parietal and frontal neglect patients. But the critical difference between groups might now be the influence of afferent inputs from the hand upon visual biases, rather than a specifically motor bias impairing reach initiation in the contralesional direction for left targets. The next experiment sought to distinguish these two interpretations by means of a control task.

The control task was exactly as for the reaching task described above in terms of apparatus and stimuli, but had one crucial procedural difference. Patients now simply had to press the start key as fast as possible when a green target was detected, rather than having to reach out to press the button immediately beneath the green target as in Experiment 1. At the start of each trial, the patients depressed the start key as before, and then released it to initiate the sequence of events, while keeping their index finger in permanent contact with it. After a variable delay as before (500–1000 ms), a green target then appeared alone or with a concurrent red distractor, or there was only a red distractor (for catch trials). The task was now to depress the start key as soon as a green target was detected, while withholding this press-at-start response on catch trials. A button-press response was required in this new task rather than a button-release, because this helped to prevent the natural tendency of participants to inadvertently introduce a lateralized component to their movement, towards the target light.

The position of the start key was varied again just as before (Fig. 1). Indeed, the press-at-start task of Experiment 2 was actually run within the same sessions as the reaching task of Experiment 1 (as noted earlier), being presented here as a separate experiment for ease of exposition. Each patient underwent at least three blocks of one task, followed by three blocks of the other task in each session, with the order of tasks (i.e. of Experiments 1 and 2) counterbalanced across patients.

The rationale for using this press-at-start task was that the different start positions should again produce exactly the same changes in afferent inputs from the ipsilesional hand (due to feeling and seeing the hand in the location where it rested at the beginning of each trial), just as when start position was varied in Experiment 1. Thus, if the effect of start position on left neglect in our parietal group was caused by afferent inputs alone, then it should be fully replicated in the present press-at-start task. By contrast, if the influence of start position on the parietal neglect patients in Experiment 1 was really caused by the changed direction of the reaching response that had to be programmed, then we should not find the same pattern of results in the new press-at-start task,
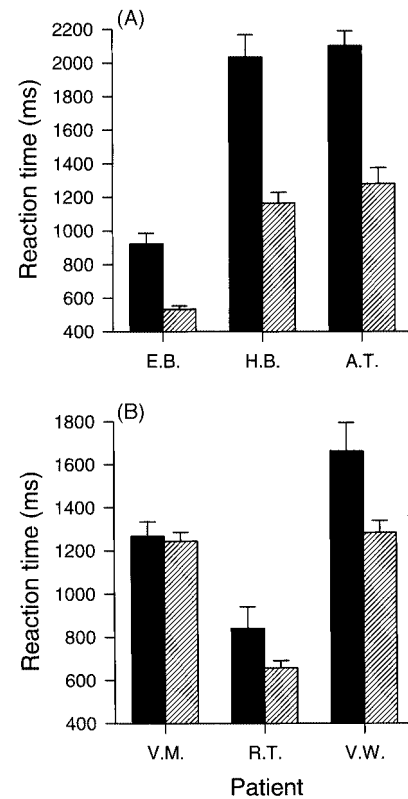

Fig. 6 Mean reaction times (with 1 SE indicated) for correct press-at-start responses to targets from centre-start position (pooled across target-only and target-plus-distractor trials), plotted separately for each patient. Solid and hatched bars represent press-at-start responses to left- and right-sided targets, respectively. (**A**) Parietal neglect patients; (**B**) frontal neglect patients. Note the different vertical scales.

since no directional reaching response was now required in any condition. Since the aim of this experiment was to test these alternative accounts for the difference between parietal and frontal neglect patients in Experiment 1, normal controls were not considered for the control task.

Results and discussion

Our initial analyses again examined whether there was any significant RT difference for left and right targets with a central start. Independent-samples *t*-tests were conducted separately for each patient, entering every trial as an observation, comparing correct RTs to left versus right targets (collapsed across distractor presence). As shown in Fig. 6, all patients were slower on average to initiate key-presses to left versus right targets at the central start. The *a priori* prediction of slower RTs to left versus right targets was confirmed individually for all patients ($P < 0.05$) except V.M. (Fig. 6). The slowness to respond to left targets presumably reflects a purely visual component of spatial neglect for these patients, since no spatially directed reach was required in the new task.
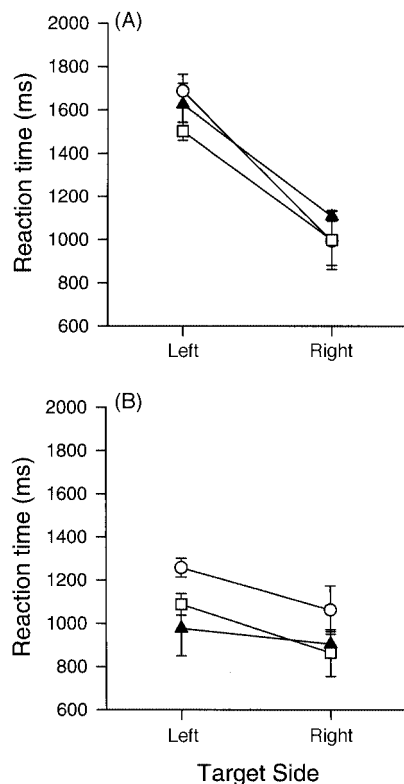
Fig. 7 Mean reaction times (±1 SE) for correct reaches to left- and right-sided targets (pooled across target-only and target-plus-distractor trials) plotted as a function of start position. Solid triangles, open circles and open squares represent data from left-, centre- and right-start positions, respectively. (**A**) Parietal neglect patients; (**B**) frontal neglect patients.

Analyses of press-at-start RTs

Mean RTs are shown in Fig. 7A for the parietal neglect group and in Fig. 7B for the frontal neglect group, separated by target side and with different lines plotted for the three possible start positions. The data in these two graphs are pooled across the factor of Distractor Condition, just as for the mean reaching RTs from Experiment 1 in Fig. 4A and B. Once again, our initial analyses examined mean RTs separately for the parietal and frontal neglect groups, in repeated-measures ANOVAs with the factors of Start Position (left, centre, right), Target Side (left, right) and Distractor Condition (target-only, target-plus-distractor). For parietal neglect patients, there was a significant main effect of Target Side [$F(1,2) = 17.4$, $P = 0.05$], with RTs to contralesional targets (1605 ms) slower than RTs to ipsilesional targets (1034 ms). This reveals a component of the patients' left neglect which must be visual rather than motor (since the same detection response was now required regardless of target side). There were no further significant main effects or interactions in the parietal press-at-start data, in striking contrast to the reaching data from Experiment 1.

In particular, the two-way interaction between Start Position and Target Side now failed even to approach significance [$F(2,4) = 2.8$, $P > 0.15$]. This indicates that, in the new press-at-start task, which required no directional motor response, the RTs of parietal patients to left versus right targets were no longer affected by start position (Fig. 7A). This contrasts with the reaching task of Experiment 1, in which start position had significantly modulated the RT cost associated with left targets for parietal neglect patients (Fig. 4A).

In a comparable repeated-measures ANOVA performed on the press-at-start RT data from the frontal neglect patients, the only significant effect was a two-way interaction between Target Side and Distractor Condition [$F(1,2) = 17.4$, $P = 0.05$]. Left targets were more susceptible to distractor interference (being 146 ms slower with a right distractor) than were right targets (96 ms slower), but this applied regardless of start position, which is consistent with a purely visual component of neglect in the frontal neglect patients.

A further analysis in which Group (parietal versus frontal) was added as a between-subjects factor showed that the two patient groups did not differ significantly from one another as a function of Start Position and Target Side in the press-at-start task [$F(2,8) = 2.4$, $P > 0.10$], unlike the reaching task of Experiment 1. The only other finding involving the Group factor was a marginal two-way interaction between Group and Target Side [$F(1,4) = 5.1$, $P < 0.09$], parietal neglect patients showing a larger RT cost for left versus right targets (mean cost 571 ms) compared with frontal neglect patients (mean cost 164 ms), suggesting a more severe purely visual component of neglect in the parietal neglect group.

Errors and false alarms

Errors and false-alarm responses for the press-at-start task are tabulated separately for the two patient groups in Appendix B. As in the reaching task of Experiment 1, patients withheld their responses correctly on the vast majority of distractor-only trials, and errors (failures to respond to targets by the deadline) were also fairly infrequent. Separate repeated-measures ANOVAs on the two possible types of mistake for the parietal and frontal neglect groups, with the same factors as for the RT analyses, failed to reveal any significant terms, though there was a trend for more errors to left targets, consistent with the clinical neglect.

Conclusions from Experiment 2

Performance of the parietal neglect patients was no longer affected by hand start position, unlike Experiment 1. This change in outcome for the parietal neglect group, in the new press-at-start task, suggests that their RT pattern in the reaching task of Experiment 1 must have been due to the change in required reach direction for left targets when central versus left start-positions were used. Certainly, the results of Experiment 2 argue against any account for that parietal pattern in terms of afferent inputs from the hand simply cueing perceptual attention towards its start position.

Patients with frontal damage also showed no influence of start position in the press-at-start task (Fig. 7B), though it

should be recalled that these individuals had similarly been unaffected by hand position in the previous reaching task, unlike the parietal neglect group. The frontal neglect patients exhibited general difficulty in initiating responses for left visual targets, regardless of hand position and of whether a spatial reach was required. Furthermore, they were particularly slow to initiate responses whenever left targets were accompanied by a distractor on the right.

General discussion

The main aim of this study was to develop a new method for separating visual and motor components in unilateral neglect. As explained in the Introduction, although numerous previous studies have observed abnormal motor performance in neglect patients, it has typically remained unclear whether this was caused by perceptual or motor deficits (or both). A second aim of our study was to assess visual and motor components in both parietal and frontal neglect patients. Our review suggested that the apparent association of more anterior lesions with 'motor' deficits might be an artefact of frontal susceptibility to the highly incompatible tasks that have been used typically in spatial opposition methods. The final aim of our study was to examine how visual distractors in ipsilesional or contralesional space may modulate reaching performance in neglect patients (Behrmann and Meegan, 1998). Previous studies have shown that contralesional distractors may undergo some residual (albeit implicit) perceptual processing in neglect, but the extent to which residual processing can affect the motor system has been controversial (Cohen *et al.*, 1995; Behrmann and Meegan, 1998; Mattingley *et al.*, 1998*a*).

Directional motor-initiation impairment in parietal neglect

We varied the start position of the hand, which allowed us to change the direction of response required for a particular visual location while still allowing the hand to move directly to the seen target in a compatible manner. Our results provide evidence for a directional motor component of the biased spatial behaviour of neglect patients with right inferior parietal lesions. These individuals evidently have a disorder of initiating leftward reaches to targets in left hemispace, in addition to their visual deficit for that side of space.

In the reaching task (Experiment 1), both parietal and frontal neglect patients were slower to initiate reaches to left than right targets, from central and right starts. But as for the many past findings of biased motor performance in neglect, this finding alone cannot reveal whether the leftward disadvantage is due to a visual or motor deficit (or both). The critical new finding is that, for parietal neglect patients only, the slowness in initiating movements to left targets was dramatically reduced from a left start position, for which the reaching response was now made in an ipsilesional

(rightward) direction. Moreover, any changes in afferent inputs from the right hand at the start of each trial were controlled for in Experiment 2, where they were found to exert no influence. We therefore conclude that one component of the impairment shown by parietal neglect patients is attributable to problems in initiating motor responses in the contralesional direction with the ipsilesional hand, over and above any purely sensory bias they may also exhibit (see also Mattingley *et al.*, 1992).

This directional motor impairment for contralesional reaches to left targets found in the parietal neglect patients cannot be an inevitable consequence of all forms of neglect after right-hemisphere damage, since neglect patients with circumscribed frontal lesions did not show the same pattern. Our frontal neglect patients showed significantly slower TTs when reaching to left versus right targets, but this held regardless of movement direction, as we discuss later after considering the implications of the parietal results.

Role of inferior parietal lobe in visual control of reaching: initial planning

In Experiment 1, the poor performance of right parietal neglect patients for the left target improved if a rightward rather than a leftward reach had to be made towards it. This effect was present only in RT for initiating reaches, suggesting a deficit in the initial programming of reaches in the contralesional direction to left targets, not merely difficulties in executing a reach once it had begun. This parietal result is not consistent with the view that only more anterior damage produces motor components to neglect (e.g. Mesulam, 1981). However, it accords well with recent data from single-cell recordings in the posterior parietal cortex of awake behaving monkeys, which demonstrate parietal involvement in the initial stages of motor planning (e.g. Bracewell *et al.*, 1996; Mazzoni *et al.*, 1996; Snyder *et al.*, 1997). For example, Snyder and colleagues found that 84% of posterior parietal cortex neurons showed responses which depended on the type of movement (saccade or reach) being planned to a location in the cell's receptive field.

It should be noted, however, that while our results identify a motor initiation deficit in parietal neglect patients for the first time, the deficit seems to be only one component of their neglect. Two pieces of evidence suggest visual components also. First, in the reaching task (Experiment 1), the right parietal neglect patients incurred an RT cost when initiating leftward movements to left targets (i.e. from a central start) but not when initiating leftward movements to right targets (i.e. from a right start). Note that in both cases the leftward movements required were of the same amplitude (cf. parts A and C in Fig. 1), thus ruling out any potential confound in terms of the overall distance of the required reach. The parietal RT impairment therefore cannot be characterized as a deficit in initiating all leftward movements, regardless of visual target location. Instead, the deficit seems

specific to leftward movements towards targets in left hemispace. Secondly, parietal neglect patients were still slow to respond to left targets even in Experiment 2, for which a spatial reach was no longer required, merely a detection response. This demonstrates a purely visual impairment for left events, in addition to the directional motoric bias. Interestingly, the separate visual and motoric biases evident in the reaching task do not appear to be additive. For example, the relative slowing in response to left versus right targets from a central start was virtually identical in the reaching (694 ms) and press-at-start (692 ms) tasks for our parietal group [$t(2) = 0.95$, n.s.]. One possible explanation for this finding is that having patients inhibit spatial reaches in the press-at-start task may have been especially demanding for them, thus increasing the apparent severity of their visual bias. Further experiments will be required to clarify this issue.

Motor deficits in the execution of reaching are now well established for patients with superior parietal damage (so-called optic ataxia; Balint 1909; Perenin and Vighetto, 1988). Our experiments provide the first evidence for a specific motoric impairment after damage to the inferior right parietal lobe, affecting the initiation of movements with the ipsilesional limb, in the contralesional direction. The deficit in our inferior-parietal neglect patients seems qualitatively different to the misreaching seen in optic ataxics with superior damage. Optic ataxics with right superior parietal damage tend to show large spatial errors towards visual targets in the (peripheral) left visual field, sometimes regardless of which hand is used (Perenin and Vighetto, 1988; Perenin, 1997). By contrast, the deficit in our inferior-parietal neglect patients was only apparent in the temporal measure of reach-initiation RT, collected for reaches that invariably succeeded in contacting the target button appropriately, with no difference in TT for leftward versus rightward movements.

Optic ataxia has been incorporated into the influential view that the superior parietal lobe forms part of a 'dorsal' stream of visual processing, considered to specialize in the on-line control of spatial action (e.g. Milner and Goodale, 1995; Milner, 1998). By contrast, the inferior parietal lobe has increasingly been viewed as part of the ventral visual stream in humans (Milner and Goodale, 1995) or as a functional nexus which cannot be strictly placed in either the dorsal or the ventral stream (Milner, 1997), and may be responsible for the conscious representation of sensory inputs rather than visuomotor transformation. The present results suggest that it is premature to discount a role for the inferior parietal lobe in human motor programming. The lesions in all three of our parietal neglect patients involved the inferior parietal lobe but spared the superior parietal lobe in its entirety.

Possible role of inferior frontal lobe in visual control of reaching

The finding that the frontal neglect patients in this study did not exhibit the directional motor bias of the parietal neglect

group is intriguing, especially since several previous investigators have proposed that frontal neglect may be particularly associated with deficits in contralesional movements (Mesulam, 1981; Heilman *et al.*, 1985; Bisiach *et al.*, 1990). The frontal neglect patients did show significantly slower reach-execution times for left versus right targets, but this was regardless of hand start position (and thus movement direction). Their impairment in executing reaches therefore does not appear to be attributable to any directional motoric bias (cf. Mattingley *et al.*, 1992), but may depend instead upon the visual location of the target.

The anterior region that appears to be associated critically with neglect in humans is located in the right inferior frontal lobe (Husain and Kennard, 1996). Part of this region is the suspected homologue of the ventral premotor cortex in macaque monkeys (Jackson and Husain, 1996), which has been suggested to play a key role in the on-line visual control of reaching movements rather than their initial programming (Kurata, 1994).

Effects of visual distractors on reaching in parietal and frontal neglect

The final aim of our study was to examine whether visual distractors presented on the neglected side during reaches to an ipsilesional target, or on the ipsilesional side during reaches to a contralesional target, could affect reach initiation and completion times. Behrmann and Meegan examined whether visual information on the neglected side could affect motor performance in a selective-reaching task similar to Experiment 1, although without our critical manipulation of hand-start position (Behrmann and Meegan, 1998). They concluded that distractors on the contralesional neglected side did not interfere with reaches, whereas ipsilesional ones did, in parietal neglect patients and also in those with more extensive lesions (involving both the parietal and frontal lobes). Thus, it has been claimed that visual information on the neglected side is processed minimally, if at all, by the visuomotor system (see also Mattingley *et al.*, 1998*a*).

Overall, the distractor results we obtained are in broad agreement with this, though they suggest some points in addition. In the reaching task of Experiment 1, we found that parietal RTs were slowed by right but not left distractors. However, this pattern was unaffected by hand start position, suggesting that it depended solely on the visual location of target and distractor events, not on the direction of the required reach. The asymmetrical pattern of interference might therefore have a purely visual basis, a possibility which also applies to the findings of Behrmann and Meegan, given that they used only a central start position, and so did not vary reach direction for a given visual location (Behrmann and Meegan, 1998).

Our parietal neglect patients did show one pattern of distractor interference in the reaching task which depended on start position: distractors slowed reach initiation from left

and central starts, but if anything speeded reaches from right starts. This may have arisen because the parietal neglect group suffered, as we have argued, from difficulties in initiating leftward reaches. The extra stimulation provided by adding a distractor (so that two visual events now appeared to the left of the hand, rather than just one) may have helped to get the hand moving in the problematic direction (cf. Baylis and Baylis, 2000).

The frontal neglect patients showed more interference from right distractors than left distractors, which was particularly apparent for them in the press-at-start detection task, where it presumably had a purely visual basis. Consistent with this, the asymmetrical distractor interference in this group was not affected by hand-start position, and is thus unrelated to reach direction.

Conclusion

This investigation of sensory and motor biases in neglect has demonstrated a temporal impairment in initiating leftward movements to left targets in patients with right inferior parietal lesions. The performance of these patients on the control task, which did not require a directional reach, showed that they also suffered from a visual impairment for left hemispace, but that their motor directional bias was superimposed on this when reaching. Thus, the parietal neglect patients suffered from a combination of visual and motor impairments, which we were able to dissect using our new paradigm. The directional deficit in motor initiation was not present in neglect patients with right inferior frontal lesions, who were merely slow to execute reaches to left targets, regardless of movement direction. These results suggest a role for the human inferior parietal lobe in the initial stages of motor planning for reaches and a possible role for the human inferior frontal lobe in the execution of visually guided reaches. These conclusions are consistent with recent electrophysiological data from monkeys but challenge conventional associations of directional motor neglect with frontal structures, and of purely perceptual neglect with the parietal lobe.

Acknowledgements

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Appendix A

Number of false alarms made by parietal neglect patients in distractor-only trials as a function of Start Position and Distractor Side (Experiment 1)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Distractor Side:	Left	Right	Left	Right	Left	Right
E.B. (/10)	1	2	3	1	0	1
H.B. (/5)	1	0	0	0	0	0
A.T. (/10)	2	1	3	2	2	3
Total (/25)	4	3	6	3	2	4

Number of false-alarms made by frontal neglect patients in distractor-only trials as a function of Start Position and Distractor Side (Experiment 1)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Distractor Side:	Left	Right	Left	Right	Left	Right
V.M. (/5)	0	0	1	0	1	0
R.T. (/5)	0	0	0	0	0	0
V.W. (/10)	1	1	1	0	2	0
Total (/20)	1	1	2	0	3	0

Number of errors made by parietal neglect patients as a function of Start Position and Target Side, pooled across target-only and target-plus-distractor trials (Experiment 1)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Target Side:	Left	Right	Left	Right	Left	Right
E.B. (/40)	3	0	10	1	2	6
H.B. (/20)	10	0	4	1	7	2
A.T. (/40)	11	2	17	5	14	6
Total (/100)	24	2	31	7	23	14

Number of errors made by frontal neglect patients as a function of Start Position and Target Side, pooled across target-only and target-plus-distractor trials (Experiment 1)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Target Side:	Left	Right	Left	Right	Left	Right
V.M. (/20)	0	0	0	0	1	0
R.T. (/20)	0	0	0	0	0	0
V.W. (/40)	2	0	5	0	11	2
Total (/80)	2	0	5	0	12	2

Appendix B

Number of false-alarms made by parietal neglect patients in distractor-only trials as a function of Start Position and Distractor Side (Experiment 2)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Distractor Side:	Left	Right	Left	Right	Left	Right
E.B. (/10)	0	0	1	0	2	0
H.B. (/5)	0	0	0	0	0	0
A.T. (/10)	0	0	0	0	2	0
Total (/25)	0	0	1	0	4	0

Number of false-alarms made by frontal neglect patients in distractor-only trials as a function of Start Position and Distractor Side (Experiment 2)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Distractor Side:	Left	Right	Left	Right	Left	Right
V.M. (/5)	1	0	0	0	0	0
R.T. (/5)	0	0	0	0	0	0
V.W. (/10)	3	3	1	3	2	0
Total (/20)	4	3	1	3	2	0

Number of errors made by parietal neglect patients as a function of Start Position and Target Side, pooled across target-only and target-plus-distractor trials (Experiment 2)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Target Side:	Left	Right	Left	Right	Left	Right
E.B. (/40)	1	1	0	0	2	0
H.B. (/20)	6	0	4	0	7	2
A.T. (/40)	6	3	11	1	8	1
Total (/100)	13	4	15	1	17	3

Number of errors made by frontal neglect patients as a function of Start Position and Target Side, pooled across target-only and target-plus-distractor trials (Experiment 2)

Start Position:	Hand LEFT		Hand CENTRE		Hand RIGHT	
Target Side:	Left	Right	Left	Right	Left	Right
V.M. (/20)	0	0	0	0	1	0
R.T. (/20)	1	0	0	0	0	0
V.W. (/40)	3	2	5	3	7	0
Total (/80)	4	2	5	3	8	0