

Orienting Attention across the Vertical Meridian: Evidence from Callosotomy Patients

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Abstract

■ This study investigates whether interhemispheric interactions mediated by the corpus callosum play a role in orienting attention across the vertical meridian. Patients with complete or partial section of the corpus callosum participated in a spatial precueing task under conditions that required covert shifts of attention within or between the visual fields. Patients with complete callosal section demonstrated normal costs on invalid trials when the cue and target appeared in the same visual field. However, these patients were impaired on invalid trials in which attention had to be redirected across the vertical meridian. The between-within difference emerged only for patients

with complete callosal section; it was not evident for a patient with section restricted to the anterior two-thirds of the callosum. Control experiments demonstrated that the deficit (1) is specific to shifts across the vertical meridian, (2) is not due to shifting between left and right hemisphere, and (3) is related to the voluntary allocation of attention in response to the cue. These results suggest that interhemispheric communication, which is normally mediated by the posterior region of the corpus callosum, contributes to the efficient movement of attention between visual fields. ■

INTRODUCTION

In the human visual system each cerebral hemisphere receives a direct visual input from the contralateral hemifield, making the vertical meridian a natural boundary in the cortical representation of visual space. Each hemisphere obtains information from the ipsilateral visual field primarily via the splenium (Myers 1965; see Innocenti 1981 for review). In the absence of this input, callosotomy patients are unable to compare two geometric forms presented on opposite sides of the vertical meridian (even when one is only 0.25° from the meridian), demonstrating a sharp division between the right and left hemifields at the visual midline (Fendrich and Gazzaniga 1989).

There is evidence that the vertical meridian may also be an important boundary for the allocation of visual attention. When a visual target is preceded by a location cue in a speeded detection task, responses are faster when the target occurs at the cued location (valid trials) than when it appears at a noncued location (invalid trials). A number of reports indicate that the increase in reaction time (RT) on invalid trials relative to valid trials (i.e., costs) is greater when the cue and target are presented in different hemifields than when they occur in the same hemifield, along the horizontal meridian (Hughes and Zimba 1985, 1987; Downing and Pinker 1985; Rizzolatti et al. 1987). On the assumption that costs represent the time required to reallocate attention from

the cued location to the target location (e.g., Posner 1980), these findings suggest that reorienting attention within a hemifield is more efficient than reorienting between hemifields.

Given that the sensory representation of visual space is primarily contralateral, it is reasonable to expect that the control of visual attention is organized in a similar fashion, with the left hemisphere (LH) controlling attention in the right visual field (RVF) and the right hemisphere (RH) controlling attention in the left visual field (LVF). It follows from this idea that shifting attention across the vertical meridian may require hemispheric interactions not required for intrahemifield orienting. Such interactions could be mediated by the corpus callosum and/or by subcortical pathways. The longer response time associated with between-field trials could reflect this additional processing.

There are, however, considerations that cast doubt on the correspondence between the hemispheric division of the visual fields and the hemispheric control of spatial attention. Evidence from patients with neglect from parietal lesions indicates that unilateral damage to either hemisphere can produce a direction-specific deficit in covert orienting in both visual fields (Ladavas et al. 1989; Posner et al. 1987; see also Baynes et al. 1986). These observations suggest that each hemisphere is responsible for shifting attention in the contralateral direction on either side of the vertical meridian.

In addition, Holtzman and colleagues (Holtzman et al.

1981) found that callosotomy patients can use a precue in one hemifield to direct attention to a specific location in the opposite hemifield. These findings led Holtzman to suggest that each hemisphere has access to a crude representation of the ipsilateral visual field that is sufficient for attentional control (Holtzman 1984, 1985). If this interpretation is correct, then orienting attention between visual fields need not require communication between the hemispheres. Alternatively, Holtzman's results raise the possibility that subcortical pathways are sufficient to mediate interhemispheric interactions needed for between-field orienting.

These considerations indicate the need to clarify whether interhemispheric interactions contribute to orienting attention across the vertical meridian. The present investigation addresses the possibility that the corpus callosum mediates such interactions by examining the relative efficiency of orienting attention within and between the visual fields in the bisected brain.

Unlike the previous investigations of visual attention that have demonstrated cooperation between the bisected hemispheres, the present experiments required the hemispheres to compete for the control of attention. We compared the magnitude of costs produced by invalid cues when the cue and target appeared in the same visual field versus when they appeared in opposite visual fields. In this way we evaluated whether orienting across the vertical meridian is compromised by complete section of the corpus callosum. In a series of four experiments, we found this to be the case. Furthermore, the absence of a between-field orienting deficit in a patient with a partial section limited to the anterior two-thirds of the callosum suggests that the posterior callosum mediates covert orienting across the vertical meridian.

RESULTS AND DISCUSSION

Experiment 1

The first experiment compared the reaction time costs (defined as valid minus invalid RT; see Methods section) associated with invalid within-field and between-field trials in two patients with complete callosal section (JW and VP), one patient with partial callosotomy (SC), and in eight aged-matched controls. If sectioning the corpus callosum specifically impairs the ability to shift attention across the vertical meridian we would expect to find a disproportionate increase in response time on between-field trials.

Figure 1 presents the costs for invalid-within and invalid-between field cue conditions for the patients and controls (see Table 1 for mean RTs). The groups show similar costs on the within-field invalid trials. On between-field trials, however, the difference between the groups is striking: the patients with complete callosal section require an additional 100 msec to respond on between-field trials whereas partial callosotomy patient

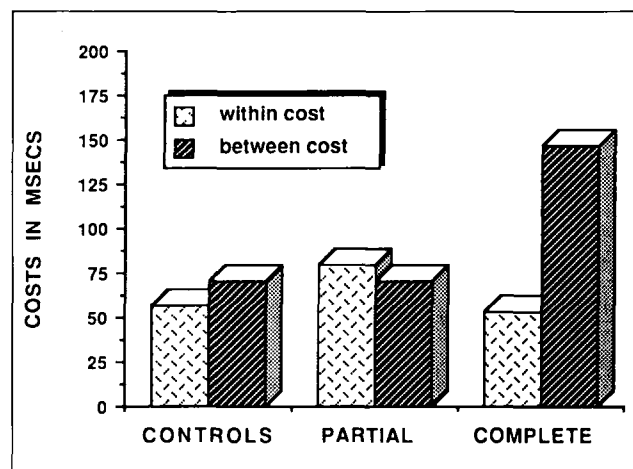


Figure 1. Costs for within and between field invalid cue conditions for control subjects, partial callosotomy patient (SC) and complete callosotomy patients (JW and VP) in Experiment 1.

Table 1. Reaction Times and Standard Deviations for Patients and Controls in Experiment 1.

		Valid	Invalid Within	Invalid Between
Controls	mean	346	405	410
	s.d.	45.9	38.4	46.4
S.C.	mean	474	552	545
	s.d.	120	132	118
J.W.	mean	531	619	681
	s.d.	154	165	189
V.P.	mean	495	573	639
	s.d.	137	98	129

SC, like the controls, shows no reliable difference between the two types of invalid trials.

Statistical analyses of the data confirmed the significance of these effects. For each patient, a separate analysis of variance (ANOVA) was performed on the reaction time data with cue condition (valid, invalid-within, invalid-between) as a fixed factor and replications as a random factor. The control data were also submitted to a one-way ANOVA with cue type as a repeated within-subjects factor.

The ANOVA for the control data revealed a significant main effect for cue condition [$F(2, 14) = 32.33; p < .001$], reflecting the fact that valid trials were significantly faster than invalid-within [$t(7) = 6.67; p < .05$] and faster than invalid-between [$t(7) = 7.23; p < .05$]. The two invalid conditions did not differ from each other. The same pattern of results emerged for partial callosotomy patient SC [$F(2, 433) = 8.06; p < .001$].

JW and VP also showed main effects for cue condition [$F(2, 1056) = 38.17; p < .0001$] and [$F(2, 323) = 12.23;$

$p < .0001$, respectively]. Paired comparisons indicate that for these patients with complete callosal section, response times are significantly slower for invalid between-field trials than for invalid-within-field trials [JW: $t(1056) = 8.98; p < .001$; VP: $t(323) = 11.9; p < .0001$].

The disproportionate increase in response times for between-field trials in patients JW and VP suggests that the absence of the corpus callosum compromises the efficiency of shifting attention between the visual fields. Furthermore, since this pattern was not observed in patient SC, our findings suggest that it is specifically the posterior third of the callosum that contributes to orienting across the vertical meridian.

Experiment 2

To establish that the impairment is specific to moving attention between the right and left visual fields, patient JW participated in two control experiments. In the first, we evaluated the orienting of attention within and between the upper and lower visual fields on each side of the vertical meridian (see Experiment 2, Methods). We expected that callosotomy would have no effect on orienting across the horizontal meridian. This expectation was confirmed: JW showed no difference in costs when orienting within versus between the upper and lower visual fields (Fig. 2 and Table 2 for mean RTs).

Experiment 3

Experiment 1 confounds the retinal vertical meridian and the boundary between right and left hemispace with respect to body-centered coordinates. Therefore the between-field costs in Experiment 1 could reflect an impairment in shifting attention between right and left

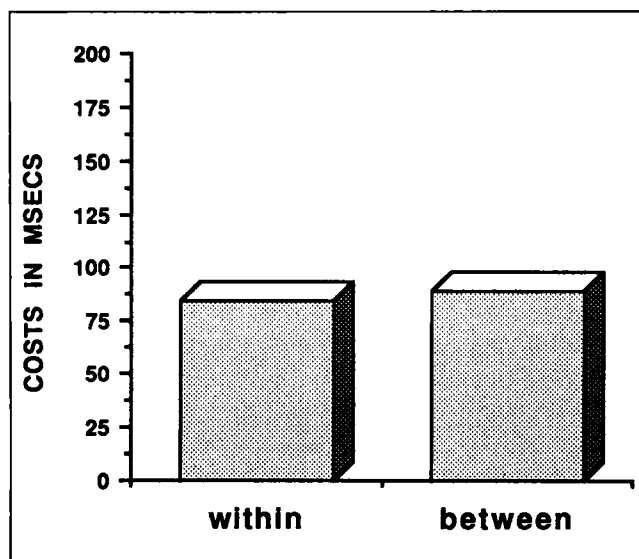


Figure 2. Costs on invalid trials associated with orienting within or between the upper and lower visual field for JW in Experiment 2.

Table 2. Reaction Times and Standard Deviations for J.W. in Experiments 2–4.

		Valid	Invalid Within	Invalid Between
Exp. 2	mean	573	658	663
	s.d.	199	150	138
Exp. 3	mean	510	587	671
	s.d.	160	150	164
Exp. 4	mean	483	512	534
	s.d.	108	118	101

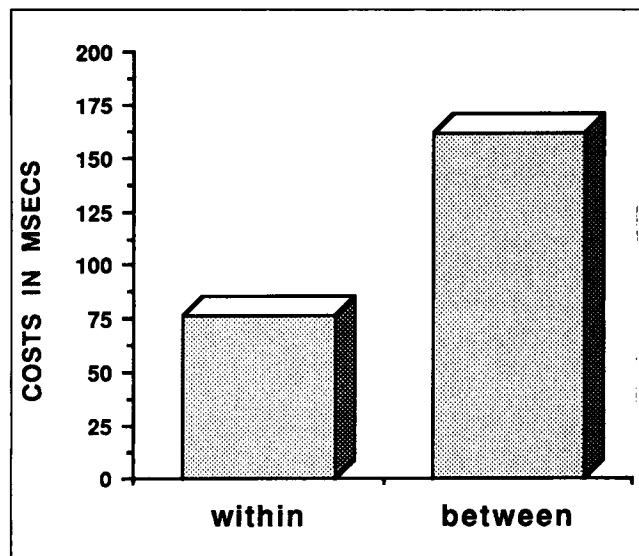


Figure 3. Costs for within- or between-field conditions with 90° head tilt for JW in Experiment 3.

hemispace. Experiment 3 tested this possibility by dissociating retinotopic and hemispatial coordinates. By tilting the head 90° and rotating the display 90°, the four target locations are aligned along the horizontal meridian of the retina, two on either side of the visual midline. Under these conditions attention shifts across the vertical meridian of the retina will correspond to shifts between upper and lower hemispace. Since Experiment 2 gave no indication of an impairment in orienting between the upper and lower hemispace, any disadvantage on between-field trials under these viewing conditions must be due to orienting across the retinal meridian. If the between-field effects observed in Experiment 1 reflect callosal control of between-field orienting, then this pattern of costs should be maintained even when retinotopic and egocentric coordinates have been dissociated.

As indicated in Figure 3, JW showed more costs on between- than within-field invalid trials, as in the first experiment. This pattern was confirmed statistically in a ANOVA that indicated a main effect for cue condition [$F(2, 29) = 6.37; p < .01$]. All three cue conditions dif-

ferred significantly from each other ($p < .05$) (see Table 2 for mean RTs).

Together the findings from the first three experiments suggest that the vertical meridian of the retina represents an important boundary in the control of selective visual attention. In particular, these observations suggest that normally the right and left hemispheres interact when attention is oriented between the visual fields and that the corpus callosum mediates aspects of this interaction.

Experiment 4

We have assumed that the impairment on between-field trials is related to the voluntary allocation of visual attention. However, an alternative interpretation might be that the cue serves as a warning signal that automatically increases the alertness of the contralateral hemisphere, leaving the uncued hemisphere in a less prepared state. If differential readiness causes the between-field effects, then the effects should not depend on the predictive validity of the cue and should emerge even when the cue provides no information about the likely location of the target. The final experiment tested this prediction by using peripheral cues that had no predictive validity.

As can be seen from Figure 4, nonpredictive cues generally reduced the costs for both within- and between-field invalid cues. The between-within difference is also substantially smaller with nonpredictive cues than in Experiments 1 and 3 where the cues were predictive. A two-way ANOVA with stimulus onset asynchrony (SOA, see Methods) and cue condition (valid, invalid-within, invalid-between) as factors revealed only a significant main effect for cue condition [$F(2, 360) = 7.84; p < .001$]. (See Table 2. Note that in the present experiment the

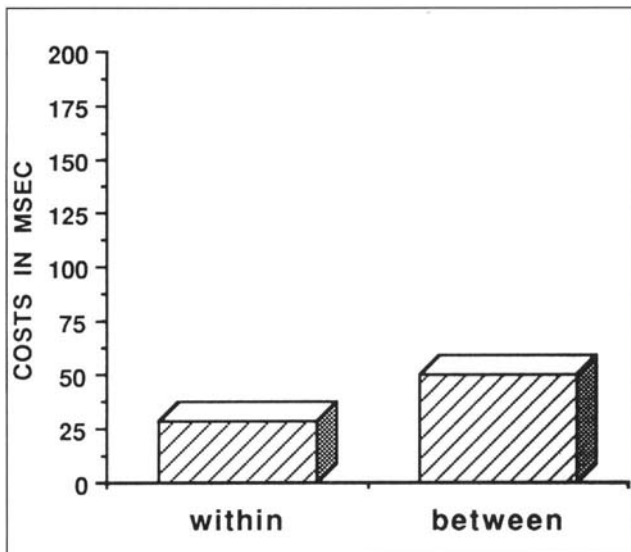


Figure 4. Costs associated with nonpredictive cues for patient JW in Experiment 4.

cues have no predictive validity, so the labels simply refer to the spatial relationship between the cue and the target.) Paired comparisons indicated that although the differences between cue conditions were small, the effects were reliable. Responses on valid trials were significantly faster than responses on invalid-within-field trials [$t(360) = 3.75; p < .001$] and invalid-within-field trials were faster than invalid-between-field trials [$t(360) = 2.9; p < .001$]. It is important to note, however, that the magnitude of the within-between difference is only 20 msec, which is a marked reduction from the differences (60–80 msec) observed in Experiments 1 and 3. These observations suggest that while some of the added costs on between-field trials may be attributable to differential alerting, the voluntary allocation of attention in response to the cue is primarily responsible for the between-field effects.

GENERAL DISCUSSION

The first three experiments indicate that for patients who have undergone complete section of the corpus callosum, the retinotopic relationship between the cued location and the target location critically determines the efficiency of attentional orienting. When the cue and target appear on opposite sides of the vertical meridian, requiring an attention shift between the right and left visual fields, callosotomy patients show disproportionate impairment in the speed of their responses to the target.

Experiment 4 indicated that when the cue had no predictive validity, in which case its effects are presumed to be involuntary (Jonides, 1981; Posner and Cohen 1981), between-field orienting was less impaired than when the cue provided useful location information. Thus, the magnitude of the between-field deficit was modulated by the attentional significance of the peripheral cue.

Relation to Other Observations with Callosotomy Patients

The present observations contrast with previous findings from callosotomy patients in a related precueing task. Holtzman et al. (1981) demonstrated that a cue delivered to one visual field can be used to orient attention accurately to a corresponding spatial location in the opposite visual field. There are, however, differences between the present experiment and Holtzman's that help to reconcile these seemingly incompatible outcomes.

In the between-field condition of the Holtzman experiment, the subject was explicitly instructed that a cue presented in one visual field would inform them of the likely target location in the opposite visual field. Thus the hemispheres were encouraged to cooperate, by whatever mechanisms remained available. Furthermore, the interval between the presentation of the cue and target was 1200 msec, thus allowing considerable time for cooperation between the hemispheres. The present

investigation was designed to test the limits of attentional integration by requiring the hemispheres to compete for the control of attention. It is evident that when one hemisphere voluntarily orients to a spatial location in response to a cue, the efficiency with which attention can be redeployed by the other hemisphere is reduced by sectioning the posterior region of the corpus callosum.

Recent work by Luck et al. (1989) suggests that callosotomy patients can search both visual fields simultaneously for a target defined by the conjunction of two features (i.e., serial search; e.g., Treisman 1982). Furthermore, this bilateral search can be executed as efficiently as a serial search in one visual field. These observations suggest that one hemisphere can deploy attention independently of the other. In contrast, the present observations suggest that the hemispheres must compete for the control of a single attentional system (see also Holtzman et al. 1984). It is important to note, however, that in the present study, marked competition was evident only when the probability was high that one hemisphere rather than the other would receive the target (e.g., Experiment 1). When the target was equally likely in either visual field (Experiment 4), interhemispheric competition was minimized. In the study by Luck et al. the target was equally likely in either visual field; in accord with the present observations, this minimized competition between the hemispheres.

Finally, based on evidence from a visual detection task without spatial precues, Gazzaniga and Ladavas (1987) suggested that each hemisphere in the bisected brain is biased to orient contralaterally. Similar observations have been made with patients with parietal damage (Kinsbourne 1987; Posner et al. 1987), and with normal subjects using line bisection (Reuter-Lorenz et al. 1990). If each hemisphere is less efficient at orienting ipsilaterally than contralaterally, then crossing the vertical meridian may be a specific instance of this more general pattern. With these considerations in mind, we analyzed JW's data from Experiment 1 to see if the within-field costs associated with contralateral orienting were smaller than those associated with ipsilateral orienting. In fact the opposite trend emerged: within each VF, ipsilateral attention shifts (toward the fovea) were faster than contralateral shifts (away from the fovea). This pattern has also been found for normal subjects using a similar paradigm (Posner et al. 1987; Fendrich and Reuter-Lorenz 1990). Thus the present findings offer no support for the view that between-field costs reflect the directional specificity of orienting control within each hemisphere.

CONCLUSION

It is well established that regions of the posterior parietal cortex play a critical role in visual orienting (e.g., Posner et al. 1984, 1987; Andersen 1987; see Jeannerod 1987 for review). Interhemispheric projections from this area

course through the posterior portion of the corpus callosum rostral to and including the splenium (Pandya and Seltzer 1986). The present finding that only those callosotomy patients with section of this region showed deficits on between-field orienting is commensurate with the possibility that interactions between left and right parietal areas are important to orienting across the vertical meridian. In the absence of the posterior callosum, alternative pathways can apparently mediate between-field orienting, but with reduced efficiency.

METHODS

Experiment 1

Subjects

Callosotomy patients JW and VP served as subjects in this experiment (see Sidtis et al. 1981, for detailed histories of these patients). JW participated in 10 blocks of 286 trials, 5 blocks with each hand. VP was run in 6 such blocks. Patient SC is a 34-year-old, left-handed male who has recently undergone section of the anterior two-thirds of the corpus callosum. He participated in four trial blocks, two with each hand. Eight nonneurological control subjects (mean age 33; range: 23–42) also participated in two trial blocks for each hand. Each block took approximately 20 min, with brief rests given every 40 trials.

Apparatus and Procedure

A microcomputer with a green monochrome monitor was used for stimulus presentation and data collection. Four horizontally aligned target locations were marked on the computer screen by 2° squares. The center-to-center distance between squares was 5°. A fixation cross was positioned midway between the second and third box, with the inner edge of these boxes 1.5° from the cross. When the subject fixated the cross, two boxes were positioned in the subject's LVF and two in the RVF.

Each trial began with a tone warning the subject to fixate the central point. Following this, one of the four locations was cued by two lines which were flashed for 200 msec above and below the box. After a 500 msec interstimulus interval, an "X" appeared in one of the boxes. The subject was instructed to press a response key as rapidly as possible when the "X" appeared. Subjects were told that the cue indicated the most likely location of the target and that they were to pay attention to that location without looking at it. Subjects were instructed to maintain central fixation from the onset of the warning tone until they responded. The experimenter sat in front of the subjects to monitor their fixation throughout the experiment.

On 70% of the trials the cue accurately predicted the target location (valid trials). On 8% of the trials the target appeared at a noncued location in the same field as the

cue (invalid-within) and on 8% it appeared in the opposite field (invalid-between). The remaining 14% of the trials were catch trials in which no target was presented.

Data Analysis

Costs represent the difference between the average RT for valid and invalid trials, rather than the difference between invalid and neutral conditions (e.g., Posner 1980). Strictly speaking then, costs in the present investigation are comprised of "costs" plus "benefits."

The data from incompatible trials in which the target was presented to the hemisphere ipsilateral to the response hand were generally slower and more variable than compatible trials in which the hemisphere receiving the target was contralateral to the response hand (see also Clarke and Zaidel 1989). The analyses we present, therefore, are restricted to the data from compatible trials; however, all effects reported were also present for the incompatible response hand. In addition, all response times greater than 3000 msec, less than 125 msec, or falling three standard deviations above or below the mean for each cue condition were eliminated. This resulted in the elimination of approximately 3% of the data.

Experiment 2

Procedure

This experiment used the same apparatus and stimulus display that was used in Experiment 1, with the following modifications. The monitor was turned 90° so that the four boxes were aligned vertically on the screen. The boxes were offset 3° to the right of the fixation point for the RVF viewing condition and 3° to the left of the fixation point for LVF viewing. JW participated in one LVF and two RVF blocks.

Experiment 3

Procedure

The stimulus display used in Experiment 1 was rotated 90° for the present experiment, as in Experiment 2. This time however, the subject (JW) also tilted his head 90° to the left so that when he fixated the central cross two boxes were positioned in the RVF and two fell in the LVF. Two blocks of trials were run with the right hand responding in both.

Experiment 4

Procedure

This experiment used the same stimulus display as Experiment 1 with two procedural modifications. First, the cue had no predictive validity, so that following its presentation, the target was equally likely to appear in any of the four target locations. Second, since the attentional

effects of nonpredictive peripheral cues normally appear only at relatively short SOAs (Posner and Cohen 1981), 50 and 350 msec SOAs were used in the present experiment. JW was told that the cue provided no information about where the target would appear. He participated in two blocks of trials, one for each hand, but as in the previous experiments, only the data from compatible trials in which the target appeared in the visual field ipsilateral to the response hand are considered.

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