

Monitoring the Visual World: Hemispheric Asymmetries and Subcortical Processes in Attention

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Abstract

■ Hemispheric specialization and subcortical processes in visual attention were investigated in callosotomy (split-brain) patients by measuring reaction times to lateralized stimuli in a spatial cuing paradigm. Cuing effects were obtained for targets presented to the right hemisphere (left visual hemifield) but not for those presented to the left hemisphere. These cuing effects were manifest as faster reaction times when the cue correctly indicated the location of the subsequent target (valid trials), as compared to trials in which the cue and target appeared in opposite hemifields (invalid trials). This pattern sug-

gests that the right hemisphere allocated attention to cued locations in either visual hemifield, whereas the left hemisphere allocated attention predominantly to the right hemifield. This finding is consistent with a body of evidence from studies in patients with cortical lesions who display different attentional deficits for right versus left hemisphere damage. Because the present pattern occurs in patients whose cerebral hemispheres are separated at the cortical level, it suggests that right hemisphere attentional allocation to events in the ipsilateral visual half-field is mediated in part via intact subcortical systems. ■

INTRODUCTION

The neural mechanisms of attention have been studied extensively in humans with focal neurological damage. A consistent finding has been that whereas lesions of either cerebral hemisphere can lead to hemispatial neglect and/or extinction, lesions of the right hemisphere produce more dramatic and consistent deficits than do similar lesions in the left hemisphere (e.g., De Renzi, 1982; Gainotti, Messerli, & Tissot, 1972; Heilman, Watson, & Valenstein, 1985; Vallar & Perani, 1987). This observation has led to the proposal that the two hemispheres differ in their control over attention to locations and objects in extrapersonal space (e.g., Heilman & Van Den Abell, 1979; Kinsbourne, 1987).

If the left and right hemispheres have different attentional capabilities, this should be evident in callosotomy patients who have undergone complete surgical resec-

tion of the corpus callosum, thereby disconnecting the cerebral hemispheres from one another at the cortical level. For example, studies in these "split-brain" patients have revealed significant lateral specializations of cognitive functions in the realms of language, speech, emotion, memory, and perception (e.g., Gazzaniga, Bogen, & Sperry, 1965; Gazzaniga, Nass, Reeves, & Roberts, 1984; Gazzaniga & Smylie, 1984; Gazzaniga, Smylie, Baynes, Hirst, & Cleary, 1984; Phelps & Gazzaniga, 1992; Sperry, Gazzaniga, & Bogen, 1969). In contrast, lateral asymmetries in visual attention have not been evident in either visual search (Luck, Hillyard, Mangun, & Gazzaniga, 1989, 1994a) or spatial cuing paradigms (e.g., Holtzman, Volpe, & Gazzaniga, 1984; Reuter-Lorenz & Fendrich, 1990) in split-brain patients, although hemispheric differences in vigilance performance have been reported (e.g., Diamond, 1979; Lådavas, Del Pesce, Mangun, & Gazzaniga, 1994).

Spatial cuing paradigms have proven to be sensitive measures of the allocation of attention. Attentional orienting is induced by means of a cue that informs the subject about where in the visual field an upcoming target stimulus is most likely to occur (e.g., Posner, 1980). The typical finding in healthy control subjects is that targets that are presented to precued locations (valid trials) elicit faster reaction times than targets presented at locations that were incorrectly precued (invalid trials). Targets preceded by cues that are uninformative (neutral trials) usually elicit reaction times that are slower than valid trials but faster than invalid trials (e.g., Posner, Synder, & Davidson, 1980). This reaction time pattern is not the result of eye movements toward or away from the anticipated target locations. In many studies, including those using discrimination accuracy measures (e.g., Hawkins, Hillyard, Luck, Mouloua, Downing, & Woodward, 1990; Luck, Hillyard, Mouloua, Woldorff, Clark, & Hawkins, 1994b), short cue-to-target intervals, and/or high-resolution monitoring of eye position (Mangun & Hillyard, 1991) have shown cuing effects to be the result of changes in attention rather than eye position.

In a cuing study with split-brain patients, Holtzman et al. (1984) presented arrow cues simultaneously to the left and right visual hemifields, thereby indicating to each hemisphere the most probable location of a subsequent target stimulus that could appear in either the left or right hemifield. On most trials both hemispheres were cued to attend to the same hemifield, and the subsequent target stimulus could appear at either the cued location (valid trial), or in the opposite hemifield (invalid trial). In addition, "neutral" trials were included in which each hemisphere was cued to expect the target in its visual hemifield. That is, the two hemispheres were given conflicting cue information; the target was then presented with equal probability to either hemifield. Each hemisphere thus received the same arrow cue on both valid and neutral trials. Moreover, for the hemisphere receiving the target, the same arrow cue and target combination were received for both valid and neutral trials. Hence, if each of the disconnected hemispheres of the split-brain patient orients attention as a function of only the cue information it receives, the valid and neutral trials in the Holtzman et al. study should have yielded equivalent reaction times.

The reaction times for valid and neutral trials were not, however, equivalent for the split-brain patient. Rather, the reaction times were slower for neutral trials than for valid trials, and slower still for the invalid cue trials. Holtzman and colleagues interpreted their results as evidence that attentional orienting to spatial locations was mediated by subcortical systems because the reaction time pattern for one hemisphere was influenced by the information presented to the other hemisphere. Thus, even though it may have been advantageous for each hemisphere to attend to the two hemifields independently in this task, the proposed subcortical atten-

tional orienting system apparently required that the two hemispheres maintain a unitary focus of attention. Although such an explanation is consistent with the results obtained by Holtzman et al. (1984), more recent data from studies of visual search in split-brain patients suggest alternative mechanisms. Luck et al. (1989, 1994a) found that split-brain patients could scan the left and right hemifields independently, thereby indicating that the two hemispheres can maintain separate attentional foci under some conditions.

In the present study we used a spatial cuing paradigm with split-brain patients to further investigate hemispheric asymmetries and interhemispheric interactions in the control of attention. The method of cuing was to present a brief lateralized stimulus (a "peripheral cue") at the to-be-attended location in the visual field (e.g., Jonides, 1981; Posner et al., 1980) (see Fig. 1). The reaction times to subsequent target stimuli could then be compared as a function of whether or not the target appeared at the cued location, which was the most probable location for target appearance. In addition, on some trials the cues provided no information about the most likely location of the upcoming target (bilateral cues and diffuse cues).

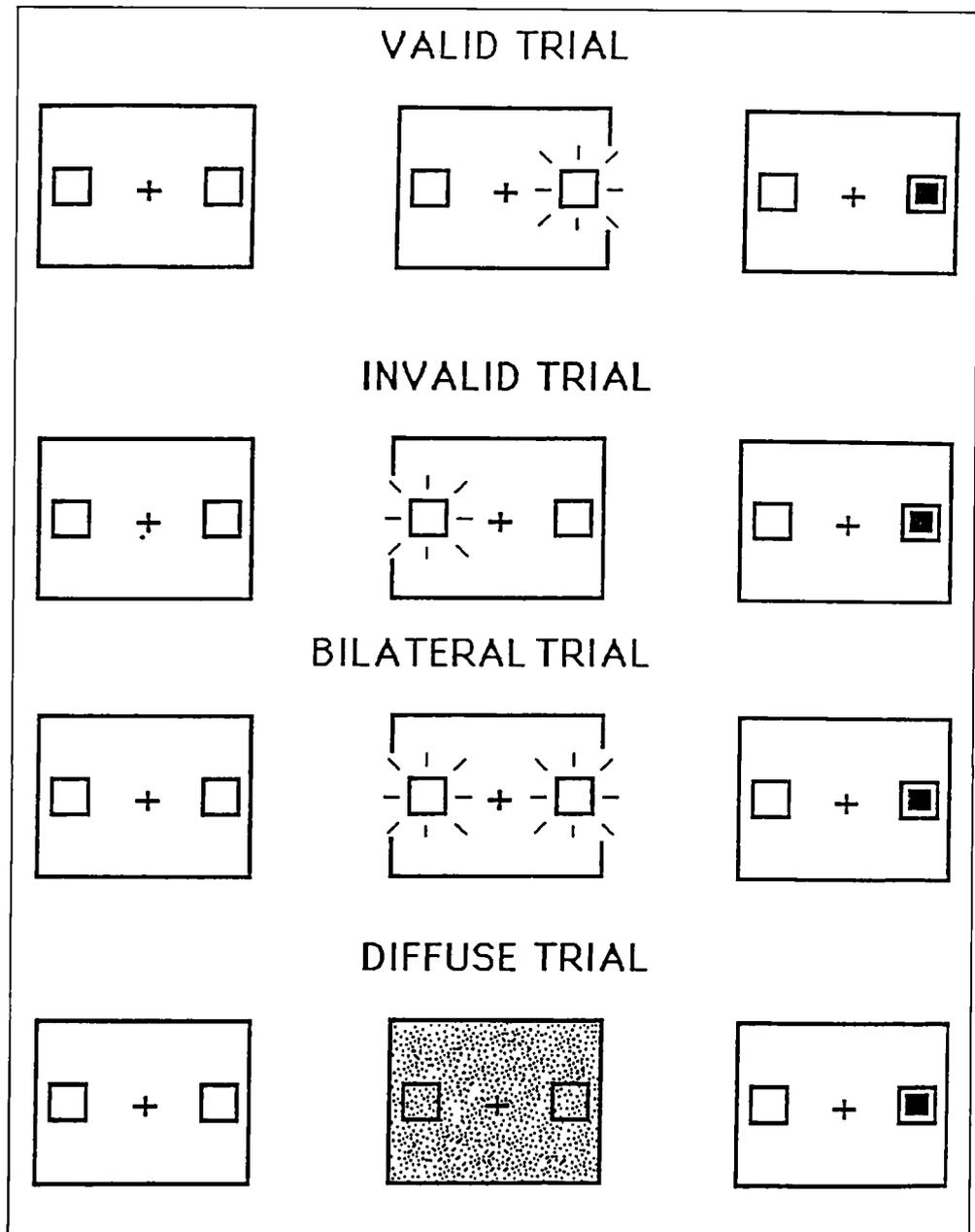
This study addressed three main issues regarding the neural substrates of attentional orienting in humans. The *first* was whether the two hemispheres would show differences in their ability to orient attention to peripheral cues. Evidence from cortical lesion data would suggest that the two hemispheres might differ in their capacities to direct attention in the visual fields (e.g., Heilman & Van Den Abell, 1979; Kinsbourne, 1987). The *second* was whether the two hemispheres would operate independently in the control of attentional orienting (e.g., Luck et al., 1994a) or whether the hemispheres would instead maintain a unitary focus of attention (Holtzman et al., 1984). If the two hemispheres could indeed orient independently, then the reaction times in the bilateral cue trials should be similar to those for the valid cue trials. The *third* issue to be investigated was the role of the corpus callosum and subcortical neural systems in attentional orienting.

RESULTS

Control Subjects

In the control subjects the RTs to the target stimuli showed a significant main effect of *cue type* [$F(3,27) = 15.3, p < 0.001$]. There were no significant differences in the effect of cue validity as a function of the hemisphere receiving the target [interaction of *hemisphere* with all four levels for *cue type*, $F(3,27) = 1.1, p > 0.3$, or with two levels of valid and invalid for *cue type*, $F(1,9) = 1.8, p > 0.2$]. RTs on valid trials (512.2 msec) were significantly faster than those on bilateral cue trials [540.4 msec, $F(1,9) = 12.3, p < 0.01$], diffuse cue trials

Figure 1. The display shown to the subjects for the four different cue types. Cues consisted of either brightenings of the outline boxes (top three panels), or a diffuse cue (bottom panel) in which random pixels across the screen were briefly illuminated. Time increments from left to right in each panel. Examples are only for right visual field targets; however, the analogous left visual field trial types were also included.



[535.4 msec, $F(1,9) = 5.2, p < 0.05$], and invalid trials [569.4 msec, $F(1,9) = 33.6, p < 0.001$]. Both the RTs to the bilateral and diffuse cue trials were significantly faster than those to the invalid trials [bilateral vs. invalid, $F(1,9) = 10.1, p < 0.02$; diffuse vs. invalid, $F(1,9) = 31.5, p < 0.001$]. None of these effects was significantly different as a function of the hemisphere receiving the target. This pattern for the controls replicates findings typically reported in the literature (e.g., Posner, 1980). Figure 2 shows the mean valid and invalid RTs for left and right field targets for the control subjects.

Split-Brain Patients

For the split-brain patients, there were significant main effects of both *cue type* [$F(3,6) = 13.6, p < 0.04$] and

band of response [contralateral vs. ipsilateral, $F(1,2) = 606.3, p < 0.002$]; collapsed over all cue validity conditions the patients were slower (708.9 vs. 654.3) to respond with the hand contralateral to the visual half-field of the target stimulus (Table 1). There was no significant main effect of *hemisphere* receiving the target, but unlike the controls, the split-brain patients showed a significant interaction of *hemisphere* and *cue type* [$F(3,6) = 25.7, p < 0.04$]. To evaluate this interaction, comparisons between pairs of cue conditions were performed separately for the left and right hemisphere (i.e., left and right visual field targets).

In general, cue validity effects were obtained only for the left field/right hemisphere targets, for which valid, bilateral, and diffuse cues led to faster RTs than did the invalid cues. RTs were significantly faster for valid versus

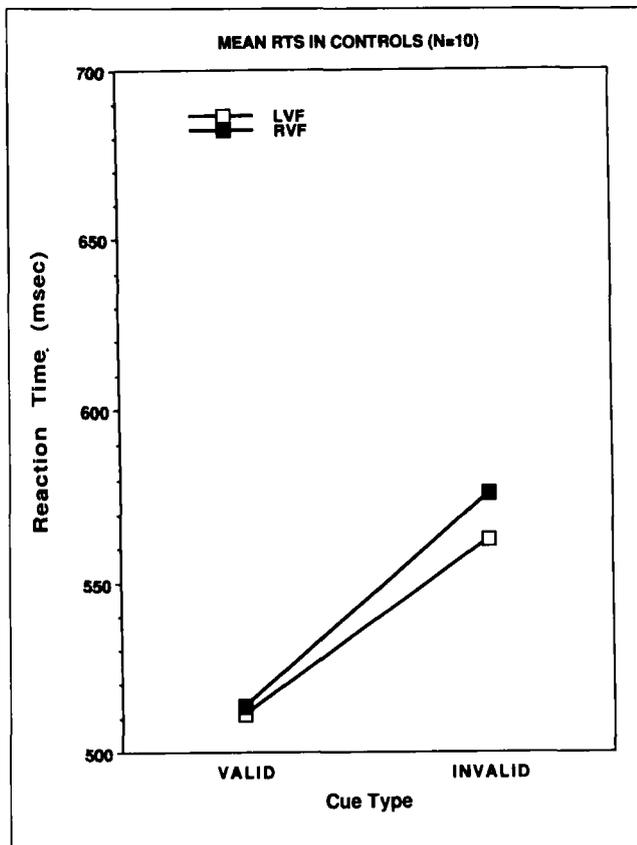


Figure 2. Mean reaction times (msec) across the 10 control subjects in response to the left visual field targets (LVF) going to the right hemisphere, and the right visual field targets (RVF) going to the left hemisphere. RTs for the controls are collapsed over the response hand when contralateral and ipsilateral to the visual hemifield of the target.

invalid cue conditions for the right hemisphere targets [$F(1,2) = 308.6, p < 0.004$], but not for the left hemisphere targets [$F(1,2) = 0.10, p > 0.7$] (Fig. 3).^{1,2} In addition, there were significant RT differences for the right hemisphere in comparisons of the valid versus diffuse conditions [$F(1,2) = 77.9, p < 0.02$], the bilateral versus diffuse conditions [$F(1,2) = 42.4, p < 0.03$], and the bilateral versus invalid conditions [$F(1,2) = 71.6, p < 0.02$]. Differences between the diffuse and invalid conditions were significant for both hemispheres, but had opposite directions (Table 1): right hemisphere, $F(1,2) = 38.1, p < 0.03$; left hemisphere, $F(1,2) = 21.1, p < 0.05$. Importantly, RTs for the valid versus bilateral cue conditions in the split-brain patients did not differ significantly for either the right [$F(1,2) = 0.7, p > 0.4$] or left [$F(1,2) = 1.4, p > 0.3$] hemispheres.

In summary, the patients responded faster to left field/right hemisphere targets that were preceded by valid, bilateral, and diffuse cues than to left field targets that were invalidly cued. In contrast, there was a general absence of cuing effects for the right field/left hemisphere targets. This pattern of hemispheric asymmetries

did not interact with hand of responses (contralateral vs. ipsilateral to the target).

DISCUSSION

The present study investigated attentional orienting in the disconnected hemispheres of split-brain patients. Hemispheric differences were assessed by measuring reaction times to cued and uncued target stimuli separately for each hemisphere. In addition, the ability of the disconnected hemispheres to orient and attend independently was examined by comparing conditions in which one versus both hemispheres were cued to orient attention to a location. The two hemispheres showed dramatic differences in the effects of spatial cuing, with the right hemisphere showing cuing effects but not the left. In addition, reaction times were just as fast on bilateral trials as on valid trials in both hemispheres. These findings are interpreted as evidence for asymmetric and independent control over visual attention by the two disconnected hemispheres of split-brain patients as detailed below.

Hemispheric Attentional Asymmetries

The asymmetries in attentional orienting observed here may be explained by postulating that the left hemisphere directs attention to the right field at all times, independent of the cue, whereas the right hemisphere allocates attention to the cued location whether in the left or right hemifield. As a result, targets appearing in the right field and processed directly by the left hemisphere are attended to equivalently during both valid and invalid trials. But in contrast, the targets appearing in the left field receive preferential attention-related processing by the right hemisphere if validly cued, and poorer processing if right hemisphere attention had previously been oriented to an invalid right field cue. Thus, in this formulation, the right hemisphere can orient to cues in either hemifield, but the left hemisphere always attends to events in the right hemifield from which it receives its direct perceptual inputs. Presumably these asymmetries are not observed in healthy controls because the corpus callosum serves to integrate attentional orienting between the two hemispheres (see Luck et al., 1994a).

This explanation of the present results implies the following. First, that the discrimination of the target was accomplished by the hemisphere that directly received the target information. The inability of split-brain patients to transfer detailed visual information between the hemispheres has been well documented (see Tramo, Baynes, Fendrich, Mangun, Phelps, Reuter-Lorenz, & Gazzaniga, 1994, for a recent review). Second, that the right hemisphere can receive information about right field events as well as left field events, and that in both cases it allocates attention to those stimuli. Presumably, this reflects the operation of subcortical pathways that can

Table 1. Mean Reaction Times (msec) to Lateral Field Targets, Collapsed across Stimulus Color in the Three Split-Brain Patients J. W., V. P., and L. B.^a

Subject	LVF Targets (left hand)				RVF Targets (right hand)			
	Valid	Bilateral	Diffuse	Invalid	Valid	Bilateral	Diffuse	Invalid
J. W.	644.9	647.5	702.4	758.2	674.1	644.5	641.3	621.6
V. P.	656.7	678.9	667.0	786.9	642.6	588.6	652.5	628.4
L. B.	601.2	606.0	678.1	709.3	596.3	582.7	656.5	637.7
Mean	634.3	644.2	682.5	751.5	637.7	605.3	650.1	629.2

Subject	LVF Targets (right hand)				RVF Targets (left hand)			
	Valid	Bilateral	Diffuse	Invalid	Valid	Bilateral	Diffuse	Invalid
J. W.	701.9	707.6	712.9	723.7	707.8	725.5	768.3	725.6
V. P.	740.6	706.3	788.4	787.2	689.4	695.5	691.2	668.8
L. B.	676.8	717.2	685.5	761.3	635.4	653.5	675.9	666.7
Mean	706.4	710.3	728.9	757.4	677.5	691.5	711.8	687.0

^aReaction times are for correct responses only and are separated as a function of hand of response using a 200–1200 msec response window. All subjects performed at above 85% accuracy for all conditions and the differences were not statistically significant among conditions.

transfer crude visual information, or information about the occurrence of events between the hemispheres (e.g., Trevarthen & Sperry, 1973). Such a possibility is suggested by studies showing that subcortical structures play an important role in attentional orienting (e.g., Rafal & Posner, 1987; Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988).

The present interpretation of hemispheric differences in attentional control is also consistent with current theories derived from studies in patients with unilateral brain damage. Specifically, the occurrence of unilateral neglect syndrome is more frequent following right hemisphere damage than following similar damage to the left hemisphere (e.g., Heilman & Van Den Abell, 1979; Heilman, Bowers, Valenstein, & Watson, 1987). One common explanation for this asymmetry is that the right hemisphere is less biased toward contralateral space than is the left hemisphere, and thus can orient attention to events occurring in either visual hemifield or hemispaces (e.g., Kinsbourne, 1987; Ládavas, 1990). The result is that damage to the left hemisphere can be partially compensated for by the undamaged, intact right hemisphere. In contrast, because the left hemisphere is more biased toward events in the contralateral hemifield and hemispaces, it cannot respond to events in the ipsilesional field following a right hemisphere lesion, resulting in an attentional deficit. Such hypotheses based upon neuropsychological studies of patients with brain damage are consistent with the data from split-brain patients presented here. The present data are also consistent with recent evidence from positron emission tomographic (PET) studies in normal human subjects that showed that

the right superior parietal cortex was activated during shifts of attentions in either direction, whereas the left hemisphere was activated only by attentional shifts in the contralateral direction (Corbetta, Miezin, Shulman, & Petersen, 1993).³

An alternative explanation for the present results might be that the two hemispheres differ in their abilities to maintain alertness and arousal (Coslett, Bowers, & Heilman, 1987; Dimond, 1979; Dimond & Beaumont, 1973; Heilman & Van Den Abell, 1979; Ládavas, De Pesce, & Provinciali, 1989; Ládavas, De Pesce, Mangun, & Gazzaniga, 1994; Posner, Inhoff, Friedrich, & Cohen, 1987; Tucker & Williamson, 1984; Wilkins, Shallice, & McCarthy, 1987). For example, if a warning cue delivered to the right hemisphere produced a generalized alerting of both hemispheres, this could lead to fast RTs for both left and right field targets. But instead, if a warning cue to the left hemisphere produced alerting only in the left hemisphere, this might lead to fast RTs for right field/left hemisphere targets, but very slow RTs for left field/right hemisphere targets because in this latter condition the right hemisphere would not be alerted or aroused. Although an interpretation of the present hemispheric asymmetries in the effects of cue validity resulting from differences in alerting rather than orienting may be consistent with the data presented here, it does not fit with the results of cuing studies in patients with unilateral parietal lesions. In a study by Posner and colleagues (1987) it was found that lesions of the right hemisphere did not affect the ability of cues to direct attention, but rather, influenced the ability of the patients to maintain a high level of alertness during the experiment. Since

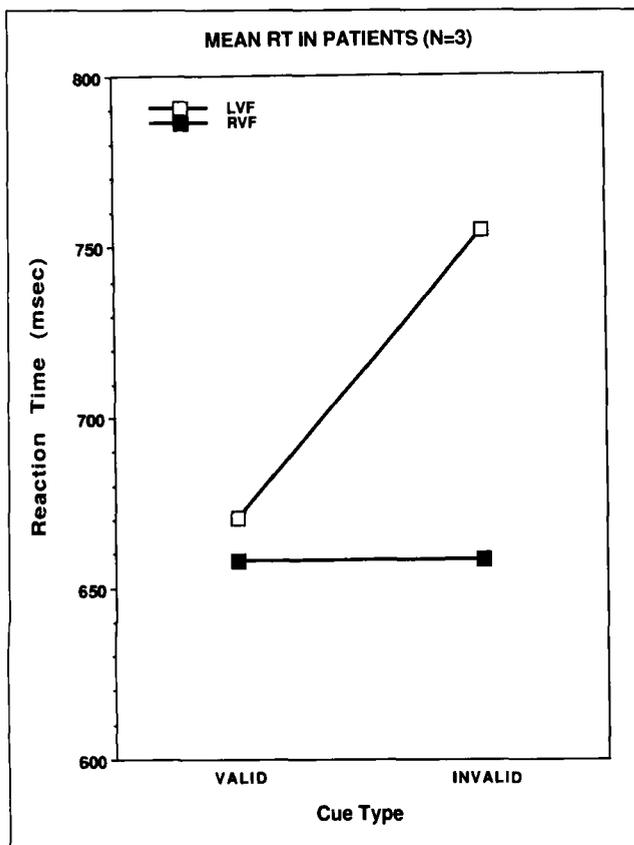


Figure 3. Mean reaction times (msec) across the three split-brain patients (J. W., V. P., and L. B.) in response to the left visual field targets (LVF) going to the right hemisphere, and the right visual field targets (RVF) going to the left hemisphere. Plotted are the RTs obtained when the hand ipsilateral to the visual hemifield of the target was used. Validly cued targets (cue and target in same hemifield) are shown at left and invalidly cued targets (cue and target in opposite hemifields) are shown at right. Split-brain patients showed significant cuing effect for LVF/right hemisphere target, but no effect for RVF/left hemisphere targets.

lesions of the right hemisphere reduce overall levels of alertness, but do not reduce the benefits of warning cues on the RTs to subsequent targets, it appears unlikely that such mechanisms could explain the present results.

Interhemispheric Interactions and Independence

In the present study using peripheral cues, evidence for independent attentional orienting of the two hemispheres was obtained. This follows because as noted above, RTs in the bilateral cue condition were as fast as RTs in the valid cue condition, suggesting that the two hemispheres did not compete for limited, unitary subcortical attentional resources in order to orient to events in the lateral fields. Additional evidence for independent attentional orienting was provided by the asymmetries in the cue validity effects. In particular, if we hypothesize that left field cues did indeed cause the right hemisphere

to orient to the left, while the left hemisphere remained oriented to the right field, this would represent the establishment of two different attentional foci in the two hemispheres. This conclusion of independent attentional orienting in the two disconnected hemispheres is consistent with the finding that split-brain patients can perform independent, parallel visual search in the two hemifields (Luck et al., 1989, 1994a). This conclusion also fits well with those studies that have indicated that each hemisphere of the split-brain patient can operate independently of the other in perceptual/attentional and mnemonic tasks. For example, Ellenberg and Sperry (1980) showed an independence in perceptual processing between the two hemispheres of split-brain patients. Similarly, Holtzman and Gazzaniga (1985) found a separation in hemispheric processing in a spatial memory task.

The present data differ significantly from those of Holtzman et al. (1984; for a review see Gazzaniga, 1987) who found evidence for a unitary focus of attention in studies employing central symbolic cues. There were several differences in the paradigms utilized in the present study and those of Holtzman and colleagues (1984), including the stimulus onset asynchrony between cue and target (1500 msec by Holtzman et al. vs. 150–600 msec in the present study), and the use of peripheral rather than central cues in the present study. Arrow cues are symbolic and require a decoding of cue information before attention can be oriented. In contrast, the peripheral cuing method consists of a sensory event whose position alone indicates the cued location. Thus, one may hypothesize that the delivery of cue information to each hemisphere is more effective using a peripheral, sensory cue. Indeed, significant differences have been shown between attention-directing cues that require a decoding of cue information prior to the orienting of attention, and cues which by their location alone indicate the likely spatial position of the subsequently presented target stimulus (e.g., Briand & Klein, 1987; Jonides, 1981; Jonides & Yantis, 1988; Müller & Rabbitt, 1989; Posner, 1980). One significant difference is that the latter have been shown to produce an early orienting of attention to the cued location that can occur automatically in the absence of any predictive value of the cue.

The method of cuing used here was, however, *predictive* of the most probable target location. As a result, we cannot assess the extent to which the effects obtained here might be the result of differences between voluntary and automatic orienting of attention in the two hemispheres. Reuter-Lorenz and Fendrich (1990) utilized peripheral cues in studies of split-brain patients and obtained significant cuing effects for both within-field and between-field cuing, but did not report the effects separately as a function of hemisphere because the study focused on other issues. They did, however, examine the influence of nonpredictive peripheral cues and found

that although significant attention effects were obtained with nonpredictive cuing, the size of the effect was greatly reduced.

CONCLUSIONS

In summary, the present data argue for an asymmetric and independent control over attentional orienting in the cerebral hemispheres. Moreover, the interaction of cue validity and hemisphere obtained in the split-brain patients is precisely the pattern that is predicted by a long literature of attentional deficits observed in patients who have suffered unilateral brain injury. The pattern suggests that the right hemisphere is sensitive to events throughout visual space, whereas the left hemisphere is strongly biased toward events in the contralateral portions of visual space. One may consider that the human right hemisphere serves as a sentry that monitors the whole of extrapersonal space in order to free the left hemisphere to undertake the dominant intellectual activities so crucial to cognition (see Gazzaniga, 1989).

METHODS

We examined callosotomy patients J. W., V. P., and L. B., and 10 normal control subjects. Each split-brain patient had undergone complete callosal transection for the treatment of intractable epilepsy. Magnetic resonance imaging (MRI) has previously verified that J. W. and L. B. received complete callosotomies. MRI findings suggest that V. P. may have a small number of residual callosal fibers in both the anterior and posterior callosal regions. The complete case histories of patients J. W. and V. P. were presented in detail in Nass and Gazzaniga (1987) and Gazzaniga and Smylie (1990), and the case history of L. B. was presented in Bogen and Vogel (1975). The control subjects were neurologically intact college students who were paid for their participation. All subjects had normal or corrected-to-normal vision.

The stimulus configurations are shown in Figure 1. Each trial began with a 50 msec duration cue that was followed after a variable interval by a target which required a rapid response by the subject. Four cue types were used: a left visual field cue, a right visual field cue, a bilateral cue (i.e., in both visual fields), or a diffuse cue in which 200 dots (2×2 pixels) randomly distributed across the entire screen were illuminated. Except for the diffuse cue, the cues consisted of a brightening of one or both of a pair of outline boxes ($2.5 \times 2.5^\circ$) that continuously demarcated the left and right target locations (6° left and right of fixation). Following the cue, a red or blue target (1.25×1.25 deg.; 50% blue and 50% red) appeared for 50 msec within one of the boxes. The stimulus onset asynchrony (SOA) from cue to target varied randomly from 150 to 600 msec, and the time from

cue onset to the onset of the next was varied at random from 2750 to 3250 msec.

When a single location was cued, the target subsequently appeared at the cued location on 80% of the trials and at the uncued location on 20% of the trials; targets appeared equiprobably at the two locations on bilateral and diffuse cue trials. The overall proportions of each of the trial types were valid = 0.45, invalid = 0.11, bilateral = 0.22, diffuse = 0.22. Subjects were required to report whether the target was red or blue by rapidly pressing one of two buttons with the thumb or index finger of one hand (hand of response counterbalanced across blocks of trials). The subjects were instructed to direct their attention to the cue because the cue indicated where the subsequent target was most likely to occur. Eye fixation was maintained on the central fixation point and was monitored by recording of the horizontal electro-oculogram (EOG). The EOG was recorded from electrodes located at the outer ocular canthi, referenced to each other, and amplified with a bandpass of 0.01–100 Hz.

Reaction times to left and right field target stimuli were compared as a function of whether the target was preceded by a valid cue (cue and target in same field), an invalid cue (cue and target in opposite fields), a bilateral cue, or a diffuse cue. Reaction times were excluded for trials with incorrect responses. Repeated-measures analysis of variance (ANOVA) was used to evaluate differences in the mean reaction times using two factors: *hemisphere receiving the target* (right vs. left) and *cue type*. Levels for the factor of *cue type* were either the four cue conditions (valid, invalid, bilateral, and diffuse) or only two cue conditions (e.g., valid versus invalid, etc.), as noted in the Results section. Both contralateral- and ipsilateral-hand responses were collapsed prior to analysis for the control subjects. For the split-brain patients, an additional factor of *hand of response* (contralateral vs. ipsilateral to target field) was included. The *p* values were corrected for heterogeneity of variance and covariance using the Greenhouse–Geisser epsilon coefficient (Jennings & Wood, 1976).

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Notes

1. The interaction of hemisphere and cue type was replicated at Dartmouth College in two of these same patients (the main

study was performed at the University of California, San Diego). Using a within-individual ANOVA with factors of *hemisphere stimulated* (right vs. left) and *cue type* (valid vs. invalid) as fixed factors, and *replications* (trials) as a random factor, the hemisphere \times cue type interaction was significant in both patients J. W. [$F(1,91) = 4.6, p < 0.04$] and V. P. [$F(1,111) = 4.1, p < 0.05$]. When comparing valid versus invalid trials, the right hemisphere showed a RT to validly cued targets of 1228 vs. 1493 msec for those invalidly cued. For the left hemisphere the RTs to validly cued targets was 1155 vs. 1087 msec for the invalidly cued targets. The replication was performed using the same stimulus parameters and procedures on a Macintosh-based computer system. Longer RTs obtained in this replication were due to both a reduced emphasis on response speed, and a much less sensitive response device than in the main study.

2. In a control experiment run at Dartmouth, one patient (J. W.) and an additional 10 normal controls were run in the same paradigm but were instructed to ignore the cue and to concentrate on speed and accuracy of the target discrimination. This latter manipulation was performed to determine whether the reaction time pattern obtained was specifically related to the instructions to utilize the cue information. The findings did not change: J. W. still showed a significant interaction between *hemisphere* and *cue type* [$F(1,104) = 10.8, p < 0.001$] that arose from the right hemisphere showing an effect of cue validity (899 vs. 1237 msec) while the left hemisphere did not (893 vs. 837 msec). The effects for the normal controls were not different from those in the main experiment in which the cue was explicitly attended.

3. The present data might also have resulted from a form of interhemispheric competition for attentional resources. Perhaps slowed reaction times to target stimuli reflect the inability of a hemisphere to allocate resources to a target because these hypothetical attentional resources were not available to it. For example, if the left hemisphere were able to gain control of limited attentional resources normally available to the both hemispheres when it received a right field cue, the result could be longer RTs to targets subsequently presented to the left field/right hemisphere. However, given the extensive literature on hemispheric difference from studies in focal cortical lesion patients (e.g., Heilman et al., 1985), and recent functional imaging findings (Corbetta et al., 1993), the most straightforward interpretation of the present pattern is that the right hemisphere is sensitive to, and/or can allocate attentional resources to events across the visual fields. In contrast, the left hemisphere is strongly biased toward events in the contralateral direction, toward the right visual half-field.

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