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Divided visuo-spatial attention systems with total and anterior callosotomy

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Abstract

The role of the corpus callosum in the inter-hemispheric integration of the visuo-spatial attention system, was investigated in patients with a total callosotomy or with an anterior callosal section. Subjects produced simple reaction times (RTs) to visual targets shown to the left or right visual hemifield. Preceding the target by an interval of 500 ms, arrow cues predicting the target location were shown left and right of the point of ocular fixation. For a majority of total and anterior callosotomy patients, results with valid focused cues (both arrows pointing to the target location) and with divided-attention cues (arrows pointing away from fixation) did not differ and both conditions produced shorter RTs than with neutral cues (equal signs). In contrast, neurologically intact subjects showed equal RTs with divided-attention and neutral cues, whereas valid focused cues produced reduced RTs relative to neutral cues. These results indicate that most split-brains, in contrast to normal observers, are capable of directing their attention to left and right visual field locations simultaneously, and therefore that each cerebral hemisphere controls its own visuo-spatial attention mechanism.

Keywords: Split-brains; Vision; Reaction time

1. Introduction

Visuo-spatial attention is an internal system concerned with the selection of items on the basis of their location within the visual field, which may operate independently of eye movements [24,27]. The parietal lobes, the putamen, and the superior colliculus are directly involved in controlling the direction of attention to specific visual field locations [e.g. see 23,25 for reviews]. Posner and his collaborators [26,28] have also suggested that the anterior portion of the brain may serve for the executive control of the posterior attentional system (i.e. the parietal lobe, putamen, and superior colliculus complex) for voluntary spatial shifts of attention [see also 18,19; but see 21]. Congruently, frontal lobe activation is observed in PET when visuo-spatial attention is oriented voluntarily, but not when it is automatically attracted by a peripheral sensory event [3]. Although distributed among different brain areas, visuo-spatial attention functions as an integrated system, the most obvious indication of which is that, in neurologically intact observers, only one focus of attention is available at any point in time [6,29]. In other words, visuo-spatial attention cannot be divided across disparate locations. What happens to the attention system when the cerebral hemispheres are separated by the surgical section of the corpus callosum,[1] is still a matter of debate. Indeed, some experiments

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[1] Surgery performed in humans for the relief of intractable epilepsy.

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suggest that callosotomy results in divided visuo-spatial attention systems, where each hemisphere controls its own focus of attention [14–17]. By contrast, other studies suggest an intact and integrated visuo-spatial attention system following callosotomy [10,11,30].

We concentrate here on two of these studies, one by Holtzman et al. [11] and the other by Mangun et al. [17], which used similar paradigms but obtained diametrically opposed results. In both studies, subjects produced speeded responses to targets lateralized to the left or right visual hemifield. Preceding the target, spatial cues providing advance information on the most probable future location of the target were presented. These directed the subject's attention toward the left or right hemifield (focused attention), or toward both hemifields simultaneously (divided-attention). Results from these conditions were compared to those with neutral cues that did not inform on the future location of the target. Split-brains ($n = 3$) in the Mangun et al. study showed, relative to neutral cues, RT benefits of equivalent size with divided-attention cues and valid focused cues. These observations indicate that, in the divided-attention condition, split-brain subjects can simultaneously attend to cued locations within the left and right hemifields, therefore suggesting that each hemisphere has its own autonomous visuo-spatial attention system. By contrast, the split-brain ($n = 1$) tested by Holtzman et al. showed equal response times (RTs) with divided-attention and neutral cues, which were both longer than with valid focused attention cues. These results argue for an integrated visuo-spatial attention system in split-brains, i.e. subjects cannot divide their attention across left and right hemifield locations at the same time.

Methodological differences between those studies may help understand the discrepant findings. In Holtzman et al., cues were pairs of arrows presented on either side of fixation and which pointed left or right. Such cues, which only have a symbolic relationship with the predicted location, have been linked to spatial shifts of attention that are under voluntary control [13,33,34]. In the study conducted by Mangun et al., spatial cues occurred directly at the location predicted by the cue — brightening of a box within which the target was to occur. Such cues appear to result in a more automatic form of orienting of visuo-spatial attention [13,33,34]. This distinction between voluntary and automatic shifts of attention may be the source for the discrepant observations of Holtzman et al. and of Mangun et al. [2].

Another important methodological difference between the studies [also pointed out in 2] concerns the stimulus onset asynchronies (SOA's) used between the spatial cue and the target. In the experiment by Holtzman et al., this interval was of 1500 ms while in the Mangun et al. study SOA's varied randomly between 150 and 600 ms. The 1500 ms SOA of Holtzman et al. is very long by any standard — significant cue validity effects can be observed with an SOA as short as 50 ms in normal observers [27]. More importantly, other studies by Holtzman's group [10,11] have shown that a cue-to-target SOA of 1500 ms is sufficient for the inter-hemispheric transfer of location information for the control of visuo-spatial attention in split-brains.[2] Such inter-hemispheric integration would prevent the visuo-spatial attention systems of each hemisphere from operating autonomously with divided-attention cues, therefore resulting in a performance which is similar to that with neutral cues. It appears likely that this is what may have occurred in the Holtzman et al. study because of the long SOA used between cue and target. By contrast, inter-hemispheric integration of conflicting location information may not have occurred with the much shorter SOA's used by Mangun et al., thus allowing each lateralized attention system of split-brains to function independently with divided-attention cues. The experiment reported here examines whether split-brains show evidence for autonomous visuo-spatial attention systems in each hemisphere if voluntary attention cues such as those used by Holtzman et al. precede the target by a relatively short cue-to-target SOA that is within the same range as that used by Mangun et al.

The above analysis suggests that, provided there are appropriate conditions, split-brains should demonstrate evidence for divided-attentional systems in a spatial cuing task. This assumption attributes a crucial role to the corpus callosum in producing the integrated visuo-spatial attention system that is evident in normal observers. If this is correct, an additional question that may be asked concerns the relative contribution of different regions of the corpus callosum in producing this integrated attention system. In the experiment reported here, we were interested in determining whether the posterior portion of the corpus callosum, which is responsible for linking the parietal lobes of each cerebral hemisphere [4,20], has a special role in this integration function. Indeed, the parietal lobes appear to be the main cortical center for the control of visuo-spatial attention [e.g. 23,25]. On these grounds, it may be predicted that patients who have had the posterior portion of their corpus callosum sectioned should show evidence for dual visuo-spatial attention

[2] In a separate experiment using the same spatio-temporal parameters as those described here, Holtzman et al. [10] have shown that the inter-hemispheric transfer of location information they have demonstrated in split-brains, is limited in use. Thus, even though it may serve for the control of visuo-spatial attention — and ocular movements [9] — split-brain subjects are incapable of overtly matching spatial locations across visual hemifields.

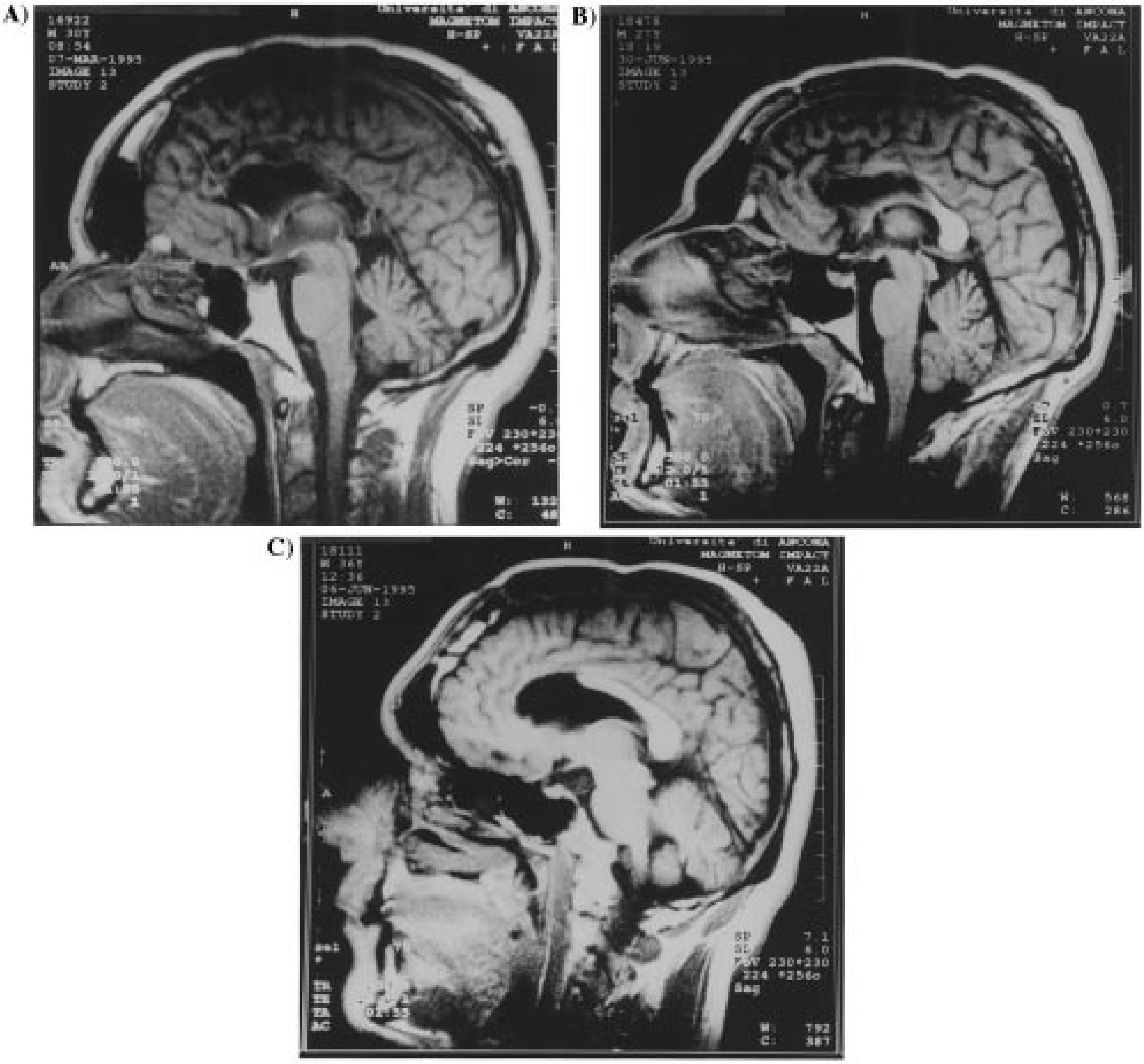

Fig. 1. Magnetic resonance image (MRI) of: (a) one of the total callosotomy patients; (b) the patient with the largest anterior callosal section; (c) the patient with the smallest anterior section.

systems. In contrast, patients with a partial callosal section sparing fibers connecting the parietal lobes of each hemisphere are expected to demonstrate an integrated visuo-spatial attention system.

2. Methods

2.1. Subjects

Ten neurologically intact individuals and 10 callosotomized subjects took part in this experiment. Seven of the callosotomized subjects had received a section of the anterior 50–80% of the corpus callosum and three a total callosal section for the relief of intractable epilepsy.

2.1.1. Neurologically intact

These subjects took part in the experiment in order to establish that the procedure used is capable of replicating the standard findings in the visuo-spatial cuing literature with valid and invalid cues, and that it can provide evidence for an integrated attention system in normal individuals. Of the ten neurologically intact subjects, four were males and six females, and eight were right-handed and two left-handed. Ages ranged from 23 to 46 y (average of 28 y). All were students at

Université de Montréal and were naive as to the purpose of the experiment.

2.1.2. Total callosotomy

The three subjects from this group were males, two right-handed and one left-handed. Their ages at the time of testing ranged from 19 to 33 y. Age of onset of epileptic symptoms ranged from 2 to 8 y and all had received a total callosal section which was performed in two steps separated by a period of about one year. In each case, the first section was restricted to the anterior part of the corpus callosum. The time separating the latest surgery from the time of testing ranged from a few months to 21 y. The full scale IQ of these subjects varied from 83 to 90. An MRI scan from one of the total callosotomy patients is shown in Fig. 1a.

2.1.3. Anterior callosal section

Three subjects in this group were females and four were males. Six of them were right-handed and one was left-handed. Their ages at the time of testing ranged from 21 to 36 y. Their epileptic symptoms began in childhood or in their teens (i.e. between the ages of 6 and 16) and, at the time of testing, the time elapsed since surgery ranged from a few months to 10 y. Full scale IQ's ranged from below 70 to 100. Fig. 1b is an MRI scan from the subject with the largest anterior section and Fig. 1c is from the subject with the smallest anterior section.

2.2. Stimuli

Subjects viewed the display screen from a distance of about 57 cm and all stimuli were shown on a white background. A fixation point (diameter of 0.5° of visual angle) displayed at the center of the screen and two empty peripheral boxes (3.0° wide × 2.1° high) centered at 5.1° left and right of fixation and aligned horizontally with it remained visible at all times throughout the experiment. Cues (0.9° wide × 0.6° high) were shown bilaterally and were centered at 1.6° from fixation. The stimuli used as cues were arrows, pointing left or right, or equal signs. Focused attention cues were made of a pair of arrows, each displayed on either side of fixation, which pointed in the same direction. Valid focused attention cues pointed toward the location that was later occupied by the target, and invalid focused attention cues pointed away from the future target location. Divided-attention cues were pairs of arrows, each shown on either side of fixation, which pointed away from fixation. Neutral cues were pairs of equal signs presented on either side of fixation. The target was an X (0.7° wide × 0.9° high) which was centered within one of the peripheral empty boxes.

2.3. Procedure

Each trial began with the onset of the cue (stimulus duration of 250 ms), which was followed 500 ms later by the target. The subject's task was to respond as quickly as possible to the onset of the target. The target remained visible until the subject produced his response. Callosotomized subjects responded by pulling a lever and neurologically intact subjects responded by pressing the spacebar on a computer keyboard. All subjects kept both hands on the response device throughout the experiment and were instructed to use either hand or both hands to respond, whichever was fastest. Subjects were also instructed to avoid anticipatory responses. The inter-trial interval was of 1500 ms. Ocular fixation was checked by an experimenter sitting behind the display screen and directly in front of the subject. All subjects were able to maintain proper ocular fixation throughout the experiment.[3]

The reason for using the kind of cooperative bimanual response described above instead of an exclusive uni-manual one was to avoid inter-manual conflict for response selection, which had the potential to interfere with manifestations of divided visuo-spatial attention systems. Indeed, previous experiments in split-brains suggest that whereas callosotomy results in divided perceptual systems [see review 2,8], response selection mechanisms may still be shared by the hemispheres[4] [5,22].

Valid focused cues occurred in 52% of trials whereas invalid, divided-attention, and neutral cues occurred in 16% of trials each. An equal number of targets for each cue type were displayed to the left or right visual hemifield. Subjects were informed of these contingencies and were instructed to direct their attention (i.e. "to look out of the corner of their eye") to the location predicted by the cue while attempting to maintain their ocular fixation on the fixation point at all times.

Callosotomized subjects were each tested in a single block of 100 trials. For these subjects, anticipatory re-

[3] The method used here for eye movement control may appear somewhat coarse. We note however that any eye movement the experimenter may have missed cannot be held responsible for our main finding, which is the significant benefit produced by divided-attention cues relative to neutral cues in split brains. Indeed, divided-attention cues were no more helpful in allowing subjects to direct their eyes to the target location than neutral cues.

[4] This preserved integration of response selection mechanisms may have been crucial in allowing split-brain patients in the studies of Holtzman et al. [11] and Mangun et al. [17] to perform the tasks they were requested. Thus, Holtzman et al. asked subjects to indicate whether target digits were even or odd and the task in the Mangun et al. study was to discriminate between targets that were red or blue. Current knowledge indicates that split-brains are incapable of effecting inter-hemispheric *perceptual* transfer of color information [12,31] or *visual* transfer of lateralized digits [1,32].

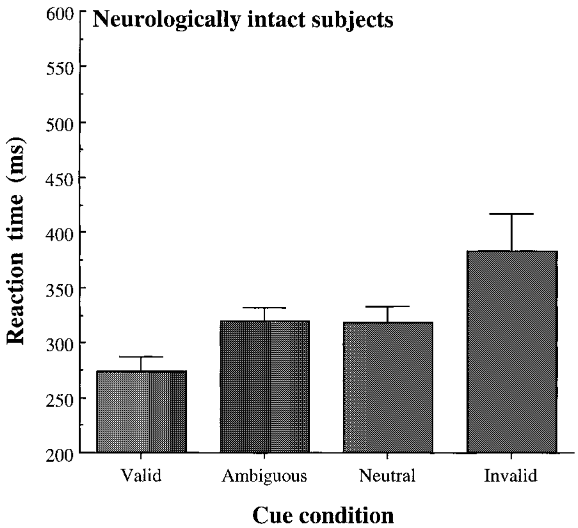

Fig. 2. Average RTs and standard errors of neurologically intact subjects ($n = 10$) in each cuing condition.

sponses (RT below 250 ms) as well as extremely high RTs (above 3000 ms) were rejected on-line and trials on which they occurred were repeated again later in the testing session. Anticipatory responses occurred in 6.0% of trials and delayed responses occurred in 1.0% of trials.

Neurologically intact subjects were each tested in a single block of 150 trials. Due to the unavailability of the equipment with which callosotomized subjects were tested, on-line rejection of anticipatory or delayed responses was not possible so this process was carried out post hoc (it is for this reason that controls were administered 150 trials instead of 100 as the split-brains). RTs lower than 150 ms[5] were rejected as anticipatory responses (5.6% of trials). As well, RTs higher than 1000 ms (0.2%) were rejected as delayed responses.

3. Results

Results from the neurologically intact subjects are shown in Fig. 2. An ANOVA applied on the RT data showed a significant effect of cuing condition [$F(3, 27) = 9.0$; $p < 0.001$]. Planned pairwise comparisons indicated, relative to neutral cues, significant benefits with valid cues [$F(1, 9) = 15.3$; $p < 0.005$] and significant costs with invalid cues [$F(1, 9) = 4.9$; $p = 0.05$].

[5] Since neurologically intact subjects were capable of responding much quicker than callosotomized subjects, the use of a criterion of 250 ms for anticipatory responses would have led to the rejection of a large number of legitimate responses, as determined by an examination of RT distributions in neurologically intact subjects. It is on the basis of these distributions that a cut-off point of 150 ms was determined for the rejection of anticipatory responses.

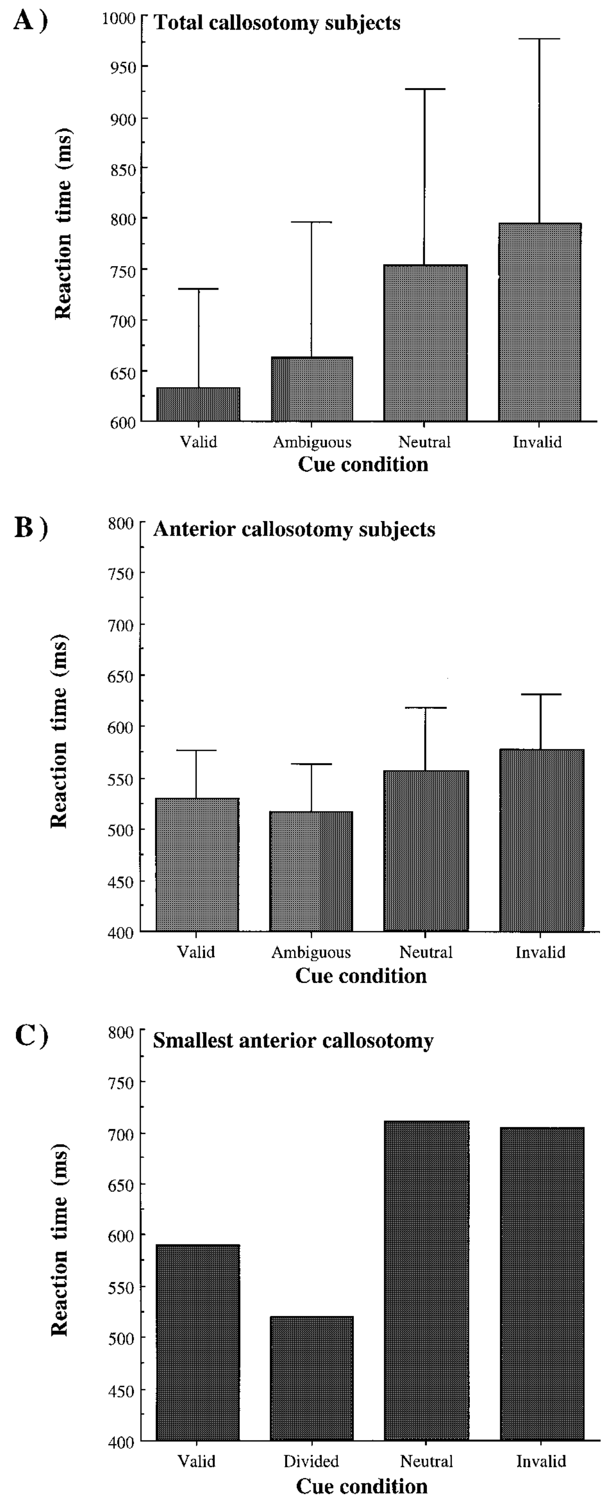

Fig. 3. Average RTs and standard errors of: (a) the group of patients with a total callosal section ($n = 3$); and (b) the group of patients with an anterior callosal section ($n = 7$). RTs in each cuing condition for the patient with the smallest anterior section are shown in (c).

RTs in the divided-attention condition (319 ms) did not differ from those in the neutral condition (318 ms; [$F(1, 9) < 1$]). These observations establish that the experimental paradigm used here replicates the standard costs/benefits typically observed in normals with valid and invalid spatial cues, respectively, and that neurologically intact subjects do show evidence for an integrated attention system, as previously demonstrated by Posner et al. [29] and by Eriksen and Yeh [6].

Fig. 3a and b show the RTs in each cuing condition for the total and anterior callosotomy groups, respectively. Note that the ranges covered by the vertical axes of these graphs differ mutually as well as from that in Fig. 2, but that their extent is the same in all figures. Analysis of these results with a two-way ANOVA of Group × Cue showed a main effect of Cue [$F(3, 24) = 5.8$; $p < 0.005$], but no main effect of Group [$F(1, 8) = 2.0$; n.s.] or interaction [$F(3, 24) = 1.5$; n.s.]. A detailed analysis of the Cue main effect compared valid, divided-attention, and invalid cue conditions to RTs with neutral cues. RTs in the valid and divided-attention conditions were shorter than those in the neutral condition [$t(8) = 2.5$; $p < 0.05$; $t(8) = 2.21$; $p < 0.05$, respectively]. However, there was no difference between results in the invalid and neutral cue conditions [$t(8) = 1.0$; n.s.]. An additional comparison between RTs with valid and divided-attention cues showed no significant difference [$t(8) = 0.02$; n.s.].

The above analyses point to divergent results from the split-brains relative to the neurologically intact subjects on the effects of invalid and divided-attention cues. More detailed analyses concentrating on these cuing effects were carried out on a case-by-case basis. RT costs from invalid cues (i.e. invalid minus neutral) for each patient were converted into z-scores by reference to the mean and standard deviation (mean = 66 ms; SD = 93) of this difference in the normal controls. This analysis indicated that none of the split-brains differed significantly from the distribution shown by the normal controls on the effect of invalid cues (z-score most different from zero = 1.5; n.s.).

Using a similar procedure, RT benefits from divided-attention cues (i.e. neutral minus RTs divided-attention) for each split-brain were converted into z-scores by reference to the mean and standard deviation (mean = −1 ms; SD = 16) of this difference in the normal controls. This analysis indicated that six of the ten callosotomized subjects studied showed a RT benefit from divided-attention cues which significantly ($p < 0.05$) departed from the distribution of this effect in the normal controls. Two of these were from the total callosotomy group ($n = 3$), who obtained z-scores of 8.0 and 8.6 ($p < 0.001$). The four others belonged to the anterior callosotomy group ($n = 7$) and their z-scores were of 2.5, 3.7, 6.8, and 11.7 (all p's < 0.05). Since significant benefits from divided-attention cues serve as an index of divided-attention systems in split-brains, it thus appears that the majority, but not all of the callosotomized subjects of the present sample show this phenomenon.

To attempt to determine the cause of this variability between callosotomized subjects on the effect of divided-attention cues, we examined whether there was any relation between evidence for divided-attention systems in a particular patient and the site of focal epileptic activity. With the exception of one case (left frontal focus), all the patients in our sample showed bilateral anomalies and an epileptic focus in either one or both temporal lobes. No subject showed focal activity outside of the temporal or frontal lobes. Most importantly, there was no site of focal activity that was unique to the subset of patients showing divided-attention, except for the one case with only a left frontal focus. It appears therefore that the location of focal epileptic activity cannot account for the variable effect of divided-attention cues among split-brains. Correlational analyses were also performed to examine the relation between the individual z-scores for the divided-attention cue effect and other personal information we had available on each subject. The potential predictor variables examined were: subject's age at test; IQ; age of onset of epileptic symptoms; age at time of surgery; time elapsed since surgery; and numbers of simple partial, complex partial, and tonic-clonic seizures and of absences per month prior to surgery. None of the correlations performed reached significance (all p's > 0.10).

Clearly, completeness of callosotomy cannot explain why some split-brains fail to show evidence for divided-attention systems since four of the seven patients with an anterior callosotomy do show the phenomenon. What perhaps is more striking is that the patient with the smallest anterior callosal section in our sample shows clear evidence for divided-attention systems with a z-score for the effect of divided-attention cues of 11.7 (Fig. 3c). Most remarkably, this patient showed, in separate tests, evidence for spared information transfer between the parietal lobes of each hemisphere. Indeed, his performance in inter-manual tactile localization is fast and accurate (51/56 correct). This observation demonstrates the functional integrity of the posterior portion of his corpus callosum.

4. Discussion

Results from the neurologically intact observers studied here replicate the standard findings in the spatial cuing literature and they show that normal subjects cannot focus their attention at two disparate spatial locations at the same time. Their focus of visuo-spatial attention is both unique and indivisible [6,29]. In the group analyses, both the anterior and total callosotomy patients diverge from the pattern of results of normal observers in two ways, they do not show an RT cost with invalid cues and they exhibit an RT benefit with divided-attention cues which does not differ from that with valid cues. The suggestion of a divergence between normal and callosotomized subjects on the effect of invalid cues is not borne out by individual data analyses, which indicate that none of the split-brains differs significantly from neurologically intact observers on this effect. By contrast, 6/10 split-brains (2/3 with total and 4/7 with anterior callosotomy) show RT benefits from divided-attention cues which significantly depart from the distribution of the effect of these cues in the normal controls. This indicates that, with divided-attention cues, these patients were able to orient their attention toward both predicted target locations simultaneously. In other words, six of the split-brains examined here provide convincing evidence for separate visuo-spatial attention systems in each cerebral hemisphere, although the four others do not.

At the outset, the main purpose of the present research was to attempt to account for the contradictory reports in the literature regarding the evidence for divided visuo-spatial attention systems after callosotomy. The factors that appeared most relevant were related to task parameters (see Introduction and [2]); specifically whether the spatial cues used are linked to automatic or voluntary shifts of attention [13,33,34], and the time interval separating the onsets (i.e. SOA) of the cue and of the target. From the results reported here, it appears that the automatic/voluntary distinction is of little relevance for explaining the discrepant findings of the literature. Thus, whereas Mangun et al. [17] provided evidence for divided visuo-spatial attention systems in split-brains using cues producing automatic shifts of attention, we provide such evidence using cues linked to voluntary shifts of attention. Cue-to-target SOA may be more important, however. Using the same cuing conditions as here but with an SOA of 1500 ms, Holtzman et al. [11] reported evidence for an integrated visuo-spatial attention system. This contrasts with the present findings as well as those of Mangun et al. [17] which were obtained using substantially shorter SOA's (500 ms and 150–600 ms, respectively). It is unlikely that this SOA effect is an artefact of between-subject variability. Indeed, the results of Holtzman et al. are based on a single subject, JW, who was also part of the Mangun et al. sample, where he showed evidence suggesting divided-attention systems (see Table 1 in [17]).

The between-subject variability observed among split-brains on the effect of divided-attention cues is a surprising finding. Indeed, assuming that the function of the corpus callosum is invariant across individuals, it was expected that callosotomy would have a comparable impact on visuo-spatial attention in all subjects. This prediction is not verified in the present results, with some split-brains showing evidence for divided-attention systems and others not. The individual data reported by Mangun et al. [17] also suggests a substantial degree of variability among split-brains in this respect. Unfortunately, no clue as to the cause of the variability among patients on the effect of divided-attention cues in the present experiment is provided by the correlational analyses relating evidence for divided-attention systems and other data we had on the split-brain subjects. It appears reasonable to suppose however that this variability among patients may be a function of pre-operative differences among patients on their reliance on the corpus callosum for inter-hemispheric integration/communication, at least for the cognitive functions studied here. Thus, pre-operatively, inter-hemispheric interactions may have largely depended on the corpus callosum in some subjects whereas it may have rested on subcortical pathways in other cases. One implication of this kind of variability is that any investigation of the effects of callosotomy may require the study of several split-brain subjects to allow generalisable conclusions.

Another unexpected outcome of the present experiment is that evidence for divided visuo-spatial attention systems was found not only in patients who had received a complete callosotomy, but also in those with a section which spared the posterior portion of the corpus callosum. According to available anatomical evidence, this callosal portion comprises fibers connecting the parietal lobes [4,20]. Since the parietal lobes are considered crucial structures for the spatial orientation of visual attention, no evidence for divided-attention systems was expected in patients with an anterior section. As demonstrated above however, some of these patients did show evidence for separate visuo-spatial attention mechanisms in each cerebral hemisphere. Two hypotheses may explain this finding.

One explanation is that, after surgery, the posterior region of the corpus callosum may have become dysfunctional, thereby resulting in functionally disconnected, albeit anatomically connected, cerebral hemispheres. This account is likely to be incorrect however. Separate evidence indicates that a section of the anterior portion of the corpus callosum has no effect on the inter-hemispheric transfer of visual information [7]. Moreover, as indicated above, the parietal lobes of our patient with the smallest anterior callosal section are still functionally connected since he can perform inter-hemispheric transfer of tactile information quickly and reliably. Despite this preserved inter-hemispheric parietal connection, his results clearly show that he can direct his attention to both visual hemifields simultaneously.

What appears as the most likely explanation for the evidence of divided-attentional mechanisms in patients with an anterior section is the cuing method. Spatial shifts of attention in response to arrow cues such as used here appear to be voluntary [13,33,34] and to involve the frontal lobes [3], which would serve to control the posterior attention system (including the parietal lobes) in orienting attention [26,28]. The fact that the frontal lobes of our patients with an anterior section were isolated from each other may have allowed them to operate autonomously and to produce a dual control system for the posterior attention mechanisms, which could thereby be oriented separately to each visual hemifield at the same time. Future studies will assess this hypothesis.

4.1. Conclusions

We have reported evidence that the majority of split-brain patients with a total or anterior callosal section are capable of orienting their visual attention to both hemifields simultaneously. This division of visuospatial attention mechanisms in split-brains contrasts with evidence from normal observers, who are incapable of dividing their attention across two distinct spatial locations at the same time. Our results therefore assign a crucial role to the corpus callosum in the functional integration of the brain areas of each hemisphere that are involved in the orientation of visuospatial attention. This function of the corpus callosum does not appear to be universal however, since the evidence available suggests that, prior to callosotomy, subcortical pathways may mediate inter-hemispheric integration/communication in a subset of patients.

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