Independent Attentional Scanning in the Separated Hemispheres of Split-Brain Patients

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Abstract

■ Previous studies of visuospatial attention indicated that the isolated cerebral hemispheres of split-brain patients maintain an integrated, unitary focus of attention, presumably due to subcortical attentional mechanisms. The present study examined whether a unitary attentional focus would also be observed during a visual search task in which subjects scanned stimulus arrays for a target item. In a group of four commissurotomy patients, the search rate for bilateral stimulus arrays was found to be approximately twice as fast as the search rate for unilateral arrays, indicating that the separated hemispheres were able to scan their respective hemifields independently. In contrast, the search rates for unilateral and bilateral arrays were approximately equal in a group of six normal control subjects, suggesting that the intact corpus callosum in these subjects is responsible for maintaining a unitary attentional focus during visual search. ■

INTRODUCTION

Evidence concerning the neuroanatomical substrates of attention has been obtained in recent years from a wide range of experimental methodologies, including functional neuroimaging, neuropsychology, and human and animal electrophysiology (see review by Posner & Petersen, 1990). These studies have implicated structures in frontal and parietal cortex that are important for the control of attention (Corbetta, Miezin, Shulman, & Petersen, 1993; Posner, Walker, Friedrich, & Rafal, 1984), structures in sensory cortical areas that are important for implementing the selection of relevant information (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Desimone, Wessinger, Thomas, & Schneider, 1990; Mangun, Hillyard, & Luck, 1993), and subcortical structures that serve as an intermediary between the higher level control systems and the lower level selection processes (LaBerge, 1993; Petersen, Robinson, & Morris, 1987).

The role of cortical–subcortical interactions in perceptual processing and selective attention can also be investigated through studies of commissurotomy ("split-brain") patients. While it is well established that the surgically separated cerebral hemispheres of these patients exhibit substantial independence in perceptual and mnemonic functions (Ellenberg & Sperry, 1980; Gazzaniga & Hillyard, 1973), there is abundant evidence that the separated hemispheres may interact with each other in the performance of concurrent sensorimotor tasks

(Kreuter, Kinsbourne, & Trevarthen, 1972; Lee-Teng & Sperry, 1974; Trevarthen, 1987). Such interactions between the divided hemispheres are presumably mediated by subcortical mechanisms that play an integrative role in coordinating the cognitive activities of the hemispheres in the absence of the corpus callosum (Sergent, 1990; Trevarthen, 1987).

Studies by Holtzman and colleagues (Holtzman, Sidtis, Volpe, Wilson, & Gazzaniga, 1981; Holtzman, Volpe, & Gazzaniga, 1984) have indicated that intact subcortical structures play an important role in integrating the attentional processes of the two hemispheres in commissurotomy patients. In one experiment (Holtzman et al., 1981), patients were given a cue in one visual field that predicted the location of a subsequent target stimulus within the opposite visual field, and reaction times were found to be faster when the target appeared at the cued location rather than an uncued location. Thus, information presented to one visual hemifield can be used to direct attention within the opposite hemifield, even in the absence of direct callosal connections between the cerebral hemispheres. In a subsequent experiment (Holtzman et al., 1984), it was found that the disconnected hemispheres could not attend to different locations simultaneously: when the two hemispheres were given conflicting cues, reaction times were slowed compared to when both hemispheres were cued to the same location. Results such as these have led to the conclusion that the disconnected hemispheres of split-brain patients

share a central, "unifocal" attention-orienting system with a limited pool of resources, presumably mediated by the intact subcortical structures (Gazzaniga, 1987; Holtzman & Gazzaniga, 1982).

The spatial cuing/speeded response task used in these experiments involves a number of processing stages, including decoding the cue, orienting attention to the cued location, perceiving and classifying the target stimulus, and selecting and executing a response. Accordingly, the interhemispheric interactions that were observed by Holtzman et al. (1981, 1984) may have arisen at any of several stages. In particular, some evidence suggests that interhemispheric interactions in commissurotomy patients may be more prevalent at the level of response selection than at the level of perceptual analysis. Thus, strong competitive interactions between the separated hemispheres have typically been observed when both hemispheres were performing tasks that required timed intermanual coordination (e.g., Kreuter et al., 1972) or imposed complex response requirements (e.g., Lee-Teng & Sperry, 1973, 1974). In addition, attentional orienting may involve a premotor component (Rizzolatti, Riggio, Dascola, & Umilta, 1987), and there is evidence for interhemispheric interaction in split-brain patients at the level of response selection and execution (Pashler et al., Submitted; Tuller & Kelso, 1989). In contrast, sensory/perceptual processing appears to occur independently in the separated hemispheres (Gazzaniga & Hillyard, 1973), and independent attentional selection may therefore be possible when response selection requirements are minimized. To test this hypothesis, we employed a visual search task that was designed to provide a more specific measure of selection at the level of perceptual processing.

In this task, subjects searched for a target item that differed from the surrounding distractor items in terms of the spatial arrangement of its component features (see Fig. 1), a task that appears to involve the serial application of attention to the individual items in the search array (Treisman & Gelade, 1980; Wolfe, Yu, Stewart, Shorter, Friedman-Hill, & Cave, 1990). To assess the presence or absence of interhemispheric attentional interactions, the search arrays were presented unilaterally on some trials and bilaterally on other trials. If the two hemispheres can search their respective visual hemifields independently, then the search rate should be twice as fast for bilateral arrays as it is for unilateral arrays. Alternatively, if the focus of attention is unitary, as proposed by Holtzman et al. (1981, 1984), then the search rate should be the same whether the items are presented to a single hemisphere or distributed between the two hemispheres.

An important advantage of this task is that the rate of attentional scanning is measured by the slope of the function relating reaction time to the number of items in the array (the "set size"), whereas other factors such as response selection time should affect the intercept of
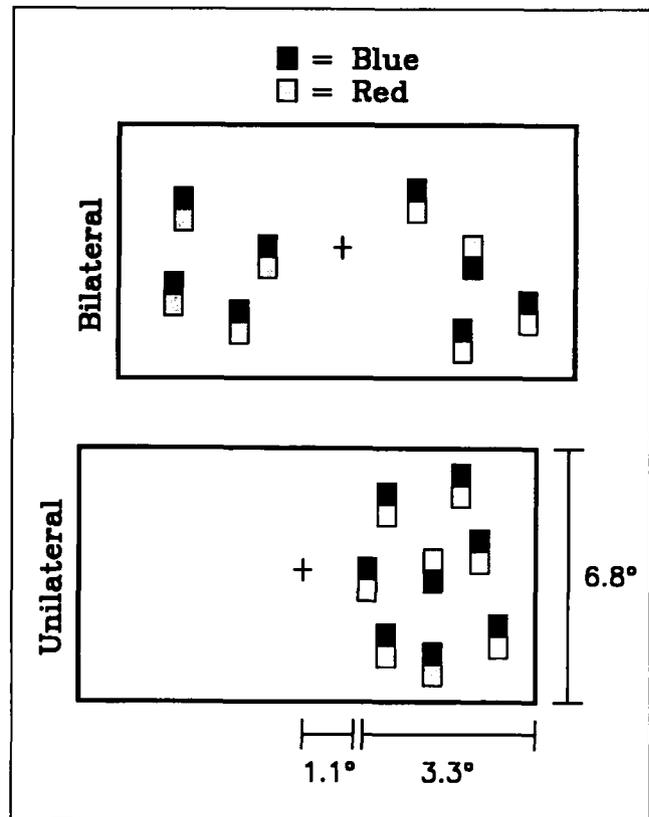

Figure 1. Example of bilateral and unilateral visual search arrays (set size 8). Note that the distance between the fixation point and the most medial search item was at least 1.1° in both cases.

this function rather than its slope (see Luck & Hillyard, 1990). As a result, interhemispheric interactions may be isolated to particular processing stages more precisely in this paradigm than in simple spatial cuing paradigms.

RESULTS

Reaction Time

The mean reaction times for the split-brain group and the normal control group are plotted in Figure 2. For both the patients and the control subjects, reaction time increased as set size increased, consistent with the hypothesis that targets are detected by means of a serial search of the stimulus arrays. Control subjects were slightly faster at detecting targets in bilateral arrays than in unilateral arrays, but the search rate, defined as the slope of the best-fit linear regression line, was very similar for bilateral (39.4 msec/item) and unilateral arrays (44.7 msec/item). In contrast, the commissurotomy patients were able to search bilateral arrays approximately twice as quickly as unilateral arrays, with search rates of 27.8 and 49.2 msec/item, respectively. Faster search rates for bilateral arrays were observed for all four of the commissurotomy patients, as shown in Figure 3.

To assess the statistical reliability of these effects, repeated-measures ANOVAs were conducted on the mean

Figure 2. Reaction time as a function of set size, averaged over subjects in the patient and control groups. The error bars indicate the standard error of the mean. Linear regression analyses were used to compute the best-fit linear search functions. Note that the *y*-axes of the two plots have different origin points, but that the scales are otherwise identical.
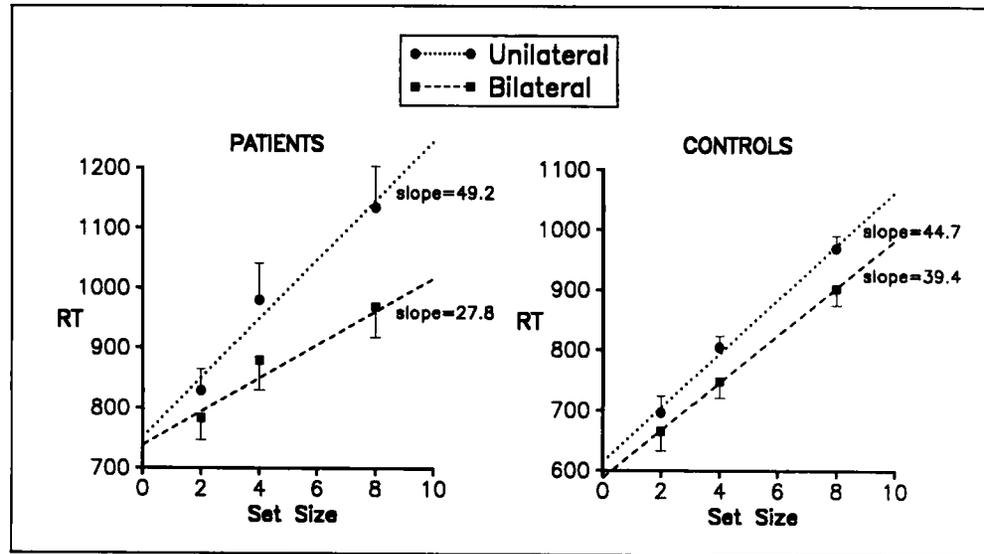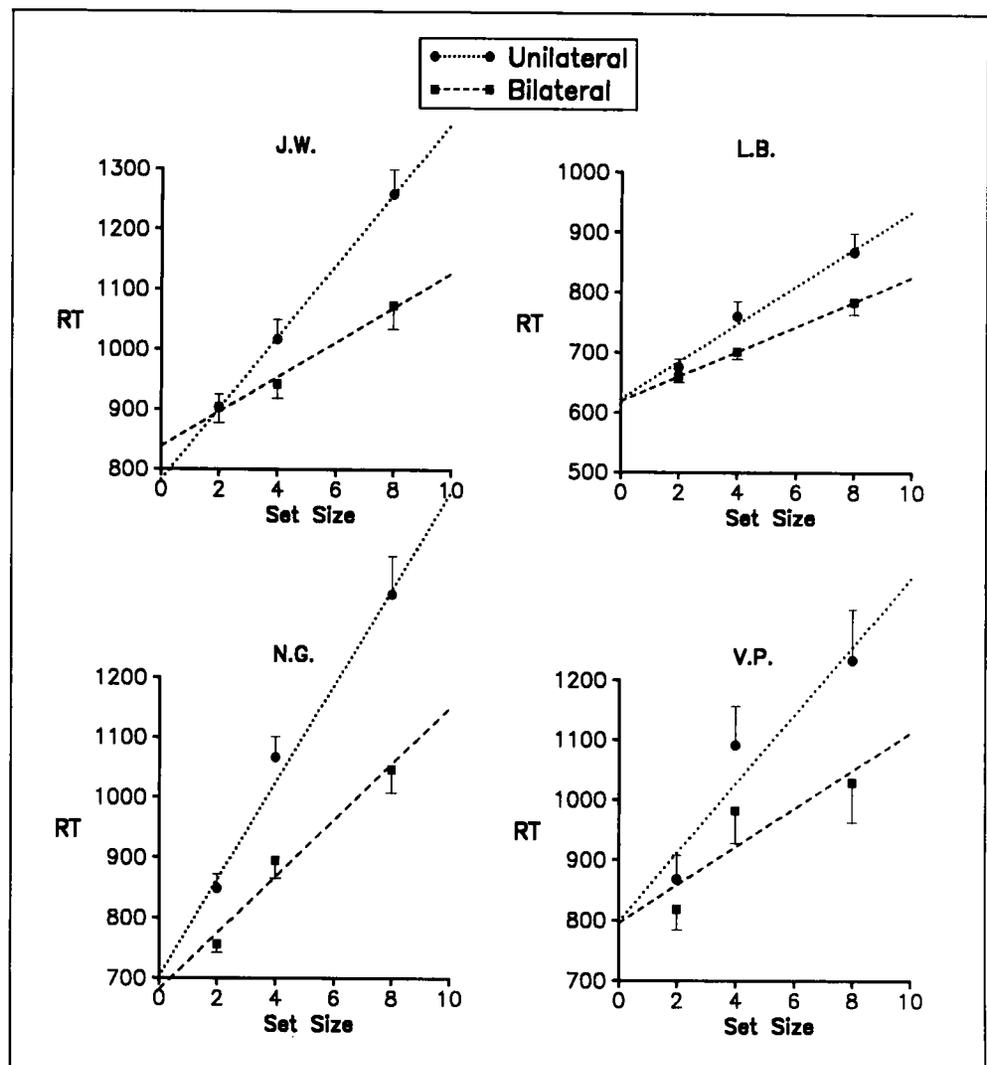

Figure 3. Reaction time as a function of set size for each of the commissurotomy patients. Error bars indicate the standard error of the mean. Note that the *y*-axes of the individual plots have different origin points, but that the scales are otherwise identical.

reaction times for the patient and control groups separately, utilizing three factors: target position (LVF or RVF), array type (unilateral or bilateral), and set size (2, 4, or 8). For the control group, there were significant main effects of set size [$F(2,10) = 24.61, p < 0.001$] and array type [$F(1,5) = 11.40, p < 0.02$], but the interaction between set size and array type did not reach significance, supporting the conclusion that the slopes for the unilateral and bilateral arrays did not differ. For the commissurotomy group, the set size and array type main effects were also significant [set size: $F(2,6) = 18.17, p < 0.005$; array type: $F(1,3) = 15.16, p < 0.03$]. In contrast to the control group, however, the set size × array type interaction was also highly significant for the commissurotomy patients [$F(2,6) = 14.94, p < 0.005$]. The reliability of this difference between the patient and control groups was assessed by including both groups in a single mixed-model ANOVA: the resulting group × set size × array type interaction was significant [$F(2,16) = 5.77, p < 0.01$], supporting the conclusion that the search slopes were greater for unilateral arrays than for bilateral arrays in the commissurotomy patients but not in the control group.

ANOVAs were also conducted on the data from each subject individually, based on the population of single-trial reaction times recorded over the course of a session. Significant set size × array type interactions ($p < 0.05$) were observed in these analyses for all of the commissurotomy patients except V.P., for whom this interaction was marginally significant ($p < 0.10$). In contrast, none of the control subjects exhibited a significant set size × array type interaction.

No significant differences in reaction time between LVF and RVF targets were observed for either the commissurotomy patients or the control group.

Accuracy

Accuracy is displayed for the patient and control groups in Figure 4, expressed as percent misses (the percentage of target-present trials on which no response was observed for the target side); false alarms occurred too infrequently to be adequately analyzed. In parallel with the reaction time results, both groups made more errors for unilateral arrays than for bilateral arrays, and this effect interacted with set size for the commissurotomy patients but not for the control subjects. Specifically, the patients' error rates increased sharply as a function of set size for unilateral stimulus arrays, but not for bilateral arrays. This resulted in a significant set size × array type interaction [$F(2,6) = 7.84, p < 0.03$] for the commissurotomy patients, whereas this interaction did not approach significance for the control group.[1] Both groups showed significant main effects of set size on error rate [patients: $F(2,6) = 7.89, p < 0.03$; controls: $F(2,10) = 24.61, p < 0.001$]. A significant main effect of array type was also observed for the control group [$F(1,5) = 11.40$,
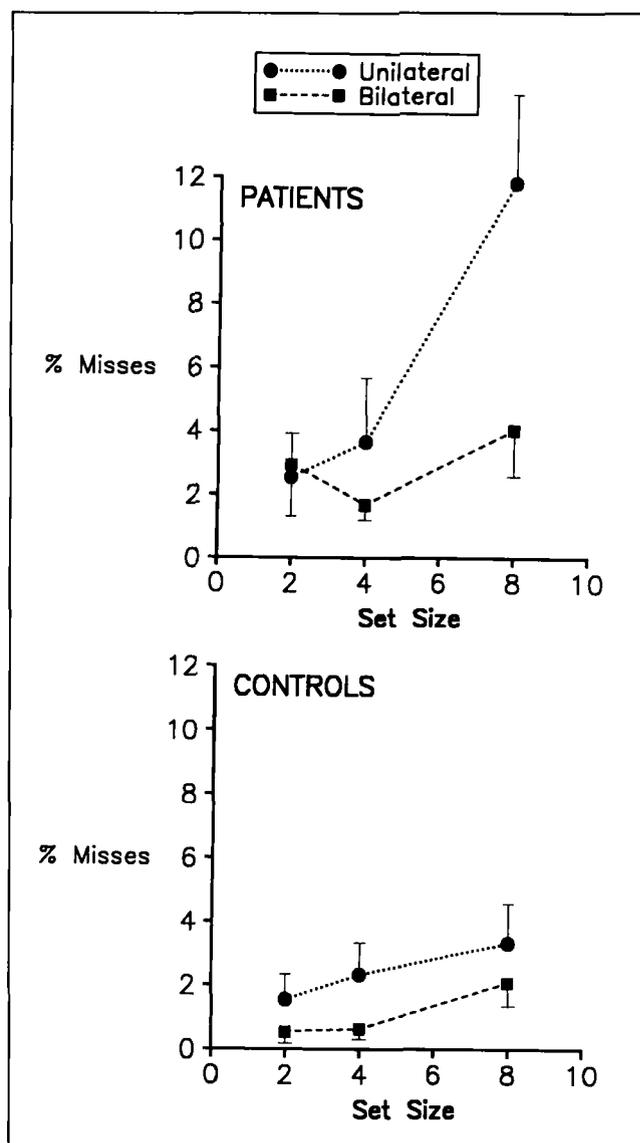

Figure 4. Accuracy (percent misses) as a function of set size, averaged over subjects in the patient and control groups. Error bars indicate the standard error of the mean.

$p < 0.02$], but did not reach significance for the commissurotomy patients. When both groups were included in a single mixed-model ANOVA, a significant group × set size × array type interaction was obtained [$F(2,16) = 5.18, p < 0.02$], indicating that the distinctive patterns of interaction between set size and array type observed in the two groups were reliably different.

As with reaction time, no significant effects involving target hemifield were observed for response accuracy in either group.

Eye Movements

An average of 21% of trials were rejected because of eye movements in the commissurotomy group, but only 8% were rejected in the control group. There was substantial intersubject variability within the commissurotomy

group, however, with almost 50% of trials being rejected for N.G. but only 7% for L.B.

Eye movements of less than 1° (approximately 10 μV) are difficult to detect in single-trial EOG data, but small, consistent eye movements can be assessed by means of signal averaging, which greatly increases the signal-to-noise ratio. Figure 5 displays such averaged EOG traces, which were time locked to stimulus onset and averaged over trials (excluding trials that were rejected from the behavioral analyses because of large eye movements). Even after the artifact rejection procedure, systematic eye movements in the direction of the target could be observed in the data from patients J.W. and N.G. However, J.W.'s eye movements averaged only about 1° of visual angle, which was less than the distance between the

fixation point and the search stimuli. Patients L.B. and V.P. showed very little tendency to move their eyes toward the target, although their behavioral results were quite similar to the other commissurotomy patients.

For those patients who exhibited eye movement deflections in the averaged EOG waveforms (N.G. and J.W.), the deflections began somewhat later for bilateral arrays than for unilateral arrays; this may have been a consequence of the fact that subjects could immediately know the visual hemifield in which the target might occur when presented with a unilateral array, but not when presented with a bilateral array. The deflections were also slightly smaller for bilateral arrays than for unilateral arrays, but the EOG waveforms for these array types were otherwise quite similar.

Figure 5. Signal-averaged horizontal EOG traces for each individual patient and for the grand average of the control subjects. Separate traces are presented for stimuli containing LVF and RVF targets, and the left and right columns show the results for unilateral and bilateral stimulus arrays, respectively. Time zero represents search array onset and positive is plotted upwards. The 10 μV scale bars in this figure correspond to a lateral eye movement of approximately 1° (positive for leftward movements and negative for rightward movements).
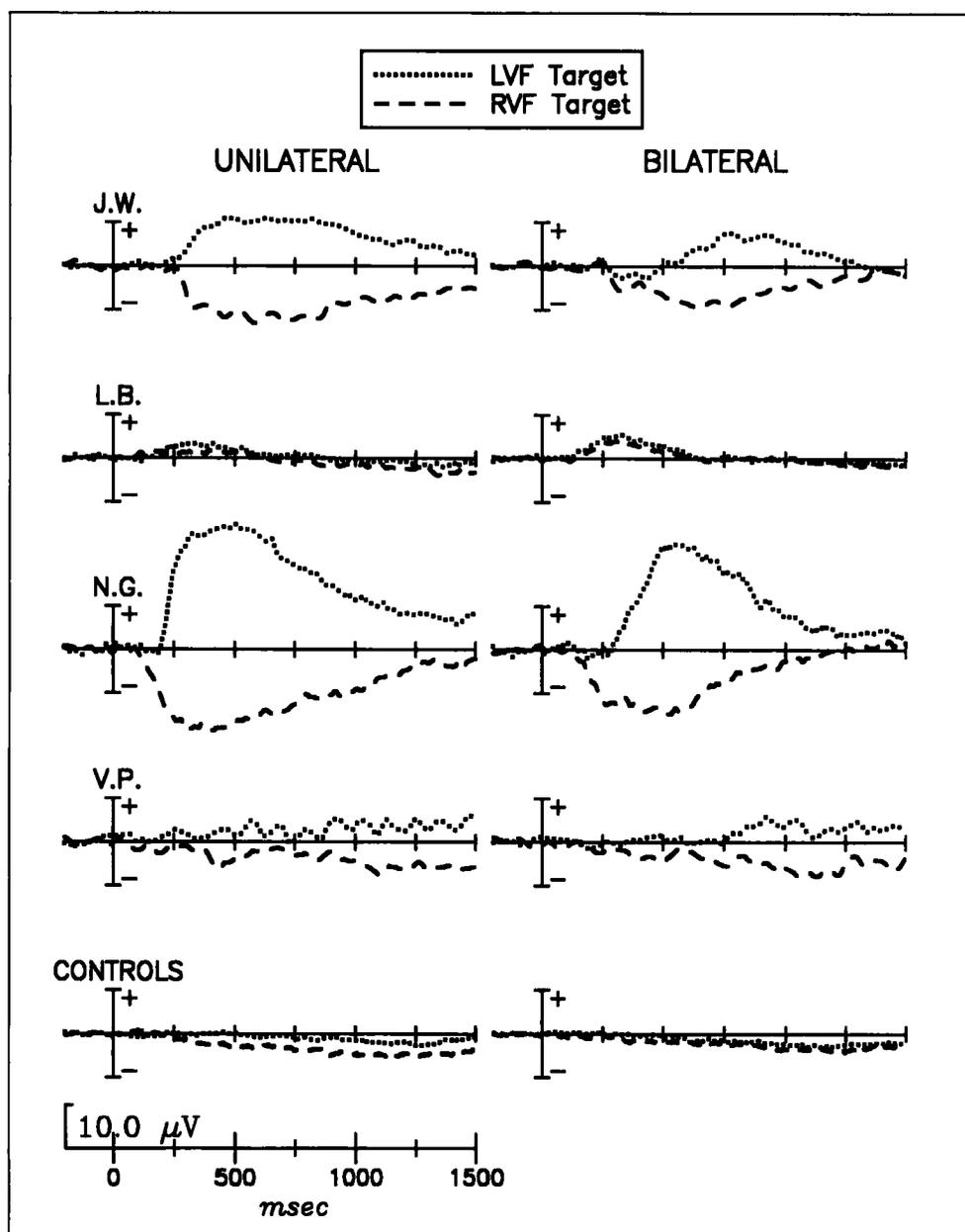
DISCUSSION

The central finding of the present study was that commissurotomy patients were able to search bilateral arrays approximately twice as fast as they could search unilateral arrays, suggesting that each of the disconnected hemispheres can independently shift its focus of attention from item to item within the contralateral visual field. In contrast, normal control subjects searched both unilateral and bilateral arrays at approximately the same rate, indicating that they could not effectively divide attention between the two visual fields. Despite their greater age, their history of seizures, and their use of anticonvulsant medication, the commissurotomy patients were actually able to search bilateral arrays at a greater rate than the control subjects, providing one of very few demonstrations of superior performance in neurological patients relative to normal controls (see also Ellenberg & Sperry, 1980; Gazzaniga & Sperry, 1966). This difference between split-brain and normal individuals indicates that the intact corpus callosum plays an important role in maintaining a unitary, integrated focus of attention across the left and right cerebral hemispheres (Ellenberg & Sperry, 1980).

To justify these conclusions, it is important to ensure that the faster search rates observed for bilateral arrays in the commissurotomy patients were not simply a result of speed–accuracy tradeoffs. If such tradeoffs were present, then the faster search rates observed for bilateral arrays should have been associated with an increase in errors. However, the error rate actually increased more rapidly for unilateral arrays than for bilateral arrays in the commissurotomy group, indicating that the reaction time effects were not a result of speed–accuracy tradeoffs. Rather, the finding of a greater increase in errors for unilateral arrays than for bilateral arrays provides further evidence that split-brain patients can search bilateral arrays more efficiently than unilateral arrays.

The possibility of eye movements must also be considered when assessing the performance of split-brain patients. In the present case, it would be difficult to attribute the results solely to shifts of gaze toward the search stimuli, because trials with large eye movements were discarded and the same behavioral effects were seen both in patients who made substantial eye movements (N.G. and J.W.) and in patients who made few eye movements (L.B. and V.P.). In addition, for those patients who did move their eyes, eye movements were present for both unilateral and bilateral arrays and were relatively small compared to the eccentricity of the stimuli. Even if these patients had performed the task by foveating the individual search items, there is no reason to believe that this would have led to faster search rates for bilateral arrays than for unilateral arrays. Indeed, a foveation strategy might be expected to lead to faster search for the unilateral stimuli, for which the hemifield containing the target could be determined immediately on stimulus onset. Thus, the behavioral results of the present experiment do not appear to be a result of eye movements.

Although faster search rates for bilateral arrays were observed only for the commissurotomy group, the control subjects did exhibit somewhat faster and more accurate responses overall for bilateral arrays than for unilateral arrays. This main effect of array type in the control subjects suggests that the left and right hemispheres may be capable of some degree of independent processing—even when the corpus callosum is intact—at some processing stage preceding or following the search process. Alternatively, this overall difference in reaction time may have been due to the greater density of stimuli in the unilateral arrays, which may have led to greater lateral inhibition.

The finding of independent attentional scanning in commissurotomy patients stands in contrast to previous spatial cuing studies in which these patients were unable to divide attention effectively between the left and right visual fields (Holtzman et al., 1984). This difference accords with previous data indicating that the type of attention-directing cues used by Holtzman et al. (1984) may not engage the same attentional mechanisms that are used during visual search (Briand & Klein, 1987).[2] In particular, reaction time effects such as those reported by Holtzman et al. (1984) may be a consequence of attention-related changes in the preparation or triggering of responses (see Mueller & Findlay, 1987; Shaw, 1984; Sperling, 1984), whereas the reaction time slope in visual search tasks appears to be more closely related to perceptual processing (Luck & Hillyard, 1990; Treisman & Gelade, 1980). Thus, the interhemispheric attentional interactions observed in the cuing experiments of Holtzman et al. (1981, 1984) may reflect competition between the separated hemispheres at output stages, while the independent search performance observed in the present experiment may reflect a separation of processing at input stages. This proposal is consistent with previous experiments demonstrating interhemispheric interactions at the level of response selection and execution (Pashler et al., 1993; Tuller & Kelso, 1989) and interhemispheric independence at the level of perceptual processing (Gazzaniga & Hillyard, 1973).

METHODS

Subjects

Four commissurotomy patients, J.W., L.B., V.P., and N.G., and a control group of six neurologically normal college students (mean age 20.2 years) served as subjects in this experiment. All of the patients underwent surgical transection of the corpus callosum (and other forebrain commissures in some cases) for treatment of epilepsy between 10 and 25 years prior to the present experiment. MRI scans have confirmed complete section of the corpus

callosum in all of these patients except V.P., in whom there remain small regions of spared fibers in the splenium and rostrum of her corpus callosum. All four of these patients have participated in a large number of neuropsychological experiments, and are highly trained at discriminating lateralized stimuli while fixating centrally. Detailed histories of these patients have been published previously (Bogen & Vogel, 1975; Sidtis, Volpe, Wilson, Rayport, & Gazzaniga, 1981).

Stimuli and Apparatus

Stimuli were presented on a color video monitor, which was placed 100 cm from the subject's eyes as he or she reclined in a comfortable chair. The visual search arrays consisted of either two, four, or eight items, each composed of a red square abutting with a blue square to form a vertically oriented rectangle subtending 0.4 × 0.8° of visual angle (see Fig. 1). Nontarget items were blue-above-red rectangles and target items were red-above-blue rectangles. The search items were placed at random locations within rectangular regions that subtended 3.3 × 6.8° and were centered 2.75° to the left or right of a central fixation point. The items were confined to the left visual field (LVF) on one-third of trials, were confined to the right visual field (RVF) on one-third of trials, and were equally distributed between the LVF and RVF on one-third of trials. The probability of a target item being present in a particular visual field (given that items were present in that field) was 0.45 for both unilateral and bilateral displays, with the constraint that a maximum of one target could appear in each stimulus array. The position of the target item was, on the average, the same for unilateral and bilateral displays. Each stimulus array was presented for 2.25 sec and followed by a 600–900 msec randomized blank interval during which only the fixation point was visible.

Lateral eye movements were measured in all subjects by means of electrooculographic (EOG) recordings. These recordings were obtained via nonpolarizable electrodes placed at the left and right lateral canthi (left eye active; right eye reference). The EOG signals were amplified with a Grass Model 12 polygraph using a bandpass of 0.01–100 Hz and stored digitally for offline analysis. A computerized eye movement detection algorithm was used to detect lateral shifts in gaze, and trials with such shifts were automatically excluded from all behavioral analyses. Because of the inherent noise in the EOG signal, some eye movements may escape detection, and stimulus-locked EOG averages were therefore obtained (after the artifact rejection procedure) to assess the presence and magnitude of such residual eye movements.

Procedure

Subjects were instructed to press a left thumb button on detecting an LVF target, a right thumb button on detecting

an RVF target, and neither button if no target was present. This procedure ensured that the sensory input and motor output required for a given visual field were lateralized to a single cerebral hemisphere. In addition, since targets never occurred in both hemifields simultaneously, responses were never required from both hemispheres at the same time. Speed and accuracy were equally stressed; responses with latencies of greater than 2500 msec were excluded from all analyses. Subjects were given extensive practice before data collection began.

Each trial block consisted of 220 stimulus presentations and included three to five short rest periods as needed. Six trial blocks were presented to each subject, resulting in a total of 108 target-present trials for each combination of set size and unilateral versus bilateral stimulus array distribution. All experimental variables (set size, unilateral/bilateral presentation, target presence, and target position) were unpredictably varied within each trial block.

Notes

1. Because single-trial accuracy is a categorical variable rather than an interval variable, individual-subject analyses of accuracy were not conducted.
2. There is also substantial evidence indicating that many of the attentional mechanisms used in visual search and spatial cuing paradigms are similar, at least at the level of perceptual processing (Luck, Fan, & Hillyard, 1993; Prinzmetal, Presti, & Posner, 1986). These tasks may therefore engage similar perceptual-level attentional mechanisms but differ in terms of postperceptual attentional processes.

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