

## DISSOCIATION OF SPATIAL INFORMATION FOR STIMULUS LOCALIZATION AND THE CONTROL OF ATTENTION

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BEHAVIOUR following complete midline section of the corpus callosum in humans, a surgical procedure preformed for the control of epilepsy, reveals intact sensory capacities within each visual half-field, but an inability to perform explicit interfield comparisons of stimuli presented on both sides of the visual midline (Gazzaniga, 1970; Gazzaniga and LeDoux, 1978). This occurs because the geniculo-striate sensory projections to areas 17 and 18 of visual cortex are almost exclusively representative of the contralateral visual half-field: ipsilateral representation is provided only indirectly through interconnections between the hemispheres *via* the corpus callosum (Choudhury, Whitteridge and Wilson, 1965; Berlucchi, Gazzaniga and Rizzolatti, 1967; Hubel and Wiesel, 1967; Rocha-Miranda, Bender, Gross and Mishkin, 1975). Loss of ipsilateral sensory representation in the isolated cerebral hemisphere following callosal section is not unique to the visual modality; analogous findings have been noted as well with regard to auditory (Springer, Sidtis, Wilson and Gazzaniga, 1978) and tactile stimulation (Gazzaniga, Bogen and Sperry, 1963).

Despite these severe sensory disconnections, corresponding disruptions of visual-motor behaviour are less evident. Commissurotomy patients direct action within the environment with little overt difficulty or hesitation: they are able to walk, run, avoid obstacles, and, in one instance, operate a motorcycle. While much of the co-ordination of such behaviour is subcortical (Grillner, 1975; Shik and Orlovski, 1976), the selection of specific goals for directed behaviour depends on internal representations and therefore, presumably, requires cortical involvement. If the separated hemispheres vied for the control of behaviour, one would anticipate an organism in a state of constant response competition. On the other hand, control of behaviour by a dominant hemisphere would predict a state of unilateral neglect. While either state can be elicited in the laboratory, neither is the rule in the normal environment. To explain the integrity of co-ordinated visual-motor behaviour, it

was suggested that, although visual information is not transferred between areas subserving explicit stimulus identification, integration may occur across the visual midline for the control of selective visual attention. By providing the commissurotomy patient with bilateral visual information for the selection of specific goals, such integration could account for the absence of both unilateral neglect and constant competition between the hemispheres for the control of directed behaviour.

The two studies reported below provided evidence that following callosal surgery, a bilateral representation of the visual world is available for the allocation of attentional capacities, and that a distinction can be made between spatial information as it is used for the control of attention and that used for explicit stimulus localization.

### *Experiment 1. Intra and Interfield Manipulation of Attention*

The paradigm employed to manipulate visual attention and measure its spatial locus was analogous to one originally proposed by Posner and his colleagues (Shulman, Remington and McClean, 1979; Posner, Snyder and Davidson, 1980; Posner, 1980). These authors noted that response latencies are reduced when an antecedent cue indicates a target's subsequent spatial location, thereby allowing observers to direct attention to the appropriate location prior to the onset of the target. Such spatial priming was shown to occur both when the cue and target appear in the same region and when the target's location has to be inferred based on a cue which appears elsewhere.

It was determined here that spatial cues effectively reduce response latencies in the commissurotomy patient, even when they require access to visual information from both visual half-fields.

**Subjects.** Two commissurotomy patients, P.S. and J.W., volunteered to serve as observers in these experiments. Both had undergone complete midline section of the corpus callosum with anterior commissure left intact. Formal testing of J.W. after callosal section revealed that he could accurately name stimuli presented to the right of central fixation, but was unable to name any stimuli presented at least 1 deg of visual angle to the left of fixation. In general, similar results have been obtained for P.S. However, this patient has an extensive right hemisphere language capacity (Gazzaniga, Volpe, Smylie, Wilson and LeDoux, 1979), and has recently demonstrated interhemispheric transfer of linguistic information. Such transfer appears to be limited to phonetically codable information, and does not represent visual transfer (Gazzaniga, Sidtis, Volpe, Smylie, Holtzman and Wilson, 1982.) Additional patient information is provided elsewhere (Wilson, Reeves and Gazzaniga, 1978; Sidtis, Volpe, Holtzman, Wilson and Gazzaniga, 1981).

**Method.** During an experimental session, the observer, seated 0.5 m from a video monitor, viewed stimuli generated and controlled by an Apple II micro-processor. Viewing was binocular and under daylight illumination. Two manual response keys were situated in front of the observer and connected to a digital timer, which allowed for the computation of response latencies.

The spatial framework for the experiment, which appeared at all times for all conditions, was provided by a computer-generated background visual display consisting of two  $3 \times 3$  cell grids located 4 deg on either side of a central fixation spot and symmetrical about the horizontal and vertical meridians (fig. 1). On all trials, one of eight equally probable target digits appeared for 150-ms in one of the cells, and the observer's task was to indicate, by pressing the appropriate key, whether the target digit was even or odd.

The observer was told that on most trials, prior to the onset of the target, a cue would appear indicating the target's subsequent spatial position. On 59 per cent of the trials in the Within-field Condition, 1.5 s before the onset of the target, an 'X' did, in fact, appear for 150 ms in the cell

corresponding to the target's spatial position (valid cue); on 12 per cent of the trials, however, the target and the cue appeared in the same grid, but within *different* cells (invalid cue); and on the remaining 29 per cent of the trials the 'X' appeared superimposed on the central fixation stimulus (neutral cue). Since both the target and cue appeared in the same visual half-field on valid and invalid trials, any benefit or cost derived from the spatial cues did not require the integration of sensory information across the visual midline.

This was not the case for the blocks of trials in the Between-field Condition. The valid spatial cue on these trials did not specify the actual location of the target but appeared, instead, in the homologous cell within the opposite grid. Analogously, the invalid cue appeared in a different relative position in the opposite grid. Thus, for between-field trials any benefit or cost derived from the spatial cues required access to visual information from both visual half-fields. In all other respects, between-field and within-field trials were identical.

Since it has been shown that the detectability of a visual stimulus can be enhanced when an antecedent visual stimulus is presented in a mirror-symmetric region of the opposite hemifield (Singer, Zihl and Pöppel, 1977), homologous rather than mirror-symmetric locations were chosen for the valid cue trials in the Between-field Condition. Likewise, we did not include invalid trials in which mirror-symmetric locations were stimulated. Thus, the efficacy of the spatial cue on between-field trials in the present paradigm required voluntary control over the locus of visual attention.

Prior to each block of trials, the observer was told whether the within-field or between-field contingency applied, and was instructed to maintain fixation of the central spot at all times. Both P.S. and J.W. are highly trained at maintaining central fixation for lateralized stimulus presentation. In order to verify that trials in which central fixation was disrupted occurred infrequently, a video camera equipped with a 10:1 zoom lens recorded the observer's eye movements throughout the experiment.

Each block of trials contained a random permutation of the representative valid, neutral, and invalid trials, with an equal number of replications in each visual half-field. Blocks of trials were presented in a counterbalanced order, and hand use was alternated between blocks.

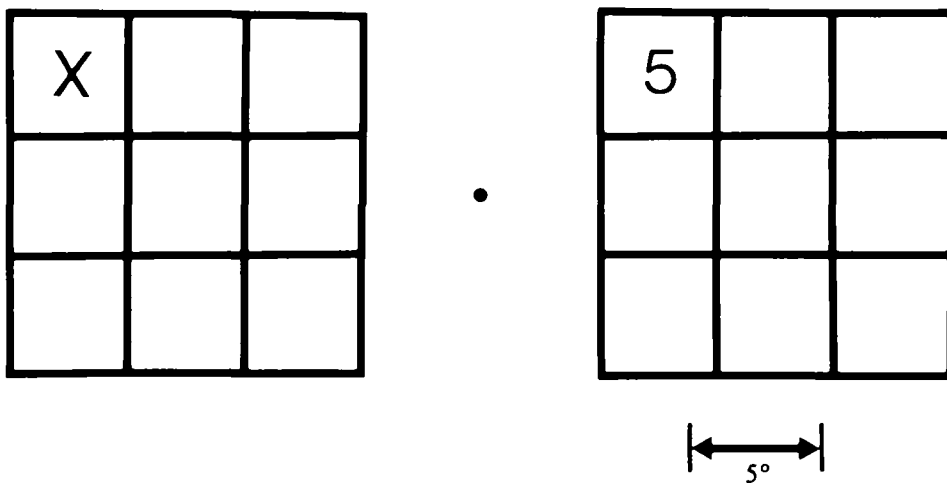


FIG. 1. Example of background visual display and stimuli for a valid cue trial in the Between-field Condition. For the initial portion of each trial, two empty grids were displayed on either side of the central fixation dot. Next, the spatial cue ('X') appeared for 150 ms in one of the grid cells. Following a 1.5 s interval, during which only the empty grids were displayed, the target digit was presented for 150 ms in the opposite grid, in the same relative position as the cue. Each square cell within a grid subtended 4 deg of visual angle, and all digits and letters, which appeared centred in these cells on experimental trials, subtended  $1 \times 2$  deg of visual angle (for description of the remaining conditions, *see text*).

### *Results and Discussion*

Response latencies on a total of 272 trials, 8 blocks of 34 trials, were collected from each observer. Approximately 7 per cent of these were excluded from the analysis because the observer responded incorrectly. An additional 4 per cent were considered 'missed' because a response did not occur within a reasonable period of time (2.0 s for P.S.; 2.5 s for J.W.), and these trials were also omitted from the analysis. Visual analysis of the video records indicated that, in fact, trials in which observers moved their eyes from central fixation to a position within a grid were very infrequent. Thus, no steps were taken to exclude these trials from the analysis. Incorrect and 'missed' trials did not vary systematically as function of condition nor did their exclusion alter the general pattern of the results for either observer.

The mean response latencies for the analysed trials, averaged across observer, visual half-field, and response hand, are summarized graphically in fig. 2. The three spatial cue types are indicated along the abscissa, and the ordinate represents the mean response latency associated with each type of trial. The data are presented separately for the Within-field Condition (filled squares) and the Between-field Condition (empty squares).

The results here are quite clearcut: response latency is reduced when the observer has prior information regarding the target's spatial location. The most striking aspect of these data is the similarity of the observers' performance under the two conditions, indicating that the spatial cue is effective both when it appears in the same visual half-field as the target and when it appears in the contralateral half-field.

Of particular interest is the detrimental effect on response latency of the invalid cue in the Between-field Condition, which implies that, when attention is directed across the midline, it is specific to the target's location and not simply directed in general to the contralateral visual half-field. If the latter alternative were the case, response latencies on valid cue trials would not be expected to differ from those on invalid cue trials. The results obtained here are quite to the contrary: performance on these two types of trials shows contrasting effects relative to the neutral cue trials.

The trends described above were supported statistically by a 3-way ANOVA (Observer X Condition X Cue Type) which revealed a highly significant main effect of cue type ( $P < 0.001$ ). In addition, the main effect of observer ( $P < 0.001$ ), and the interaction between observer and cue type ( $P < 0.005$ ) were also significant. The remaining main effect and two-way and three-way interactions were not significant. The significant difference between observers was due to shorter response latencies, overall, of observer P.S. P.S. also showed a smaller range of response latencies as a function of cue type, accounting for the significant interaction that was obtained. It should be stressed, however, that, despite the significant interaction between observer and cue type, the relative effects of the three spatial cue types on response latencies were the same for both subjects.

The observed ability of commissurotomy patients to integrate the visual half-fields for the control of attention is in dramatic contrast to their inability to perform

explicit interfield visual comparisons. It can be inferred that interfield comparisons depend primarily on visual cortex, since they are typically disrupted when posterior callosal section or damage disconnects visual cortex (Maspes, 1948; Gazzaniga and Freedman, 1973; Sugishita, Iwata, Toyokura, Yoshioka and Yamada, 1978; Levine and Calvanio, 1980; Sidtis *et al.*, 1981), but not when the lesion is restricted to the anterior callosum, in which case occipital interconnections are spared (Sweet, 1941; Geschwind and Kaplan, 1962; Gordon, Bogen and Sperry, 1971; Gazzaniga, Risse, Springer, Clark and Wilson, 1975). The present data imply that, in contrast, visual information for the control of attention projects to brain structures that maintain functional bilateral visual representation following callosal section. Thus, in the present paradigm, it was predicted that bilateral visual information would not be available for explicit stimulus localization.

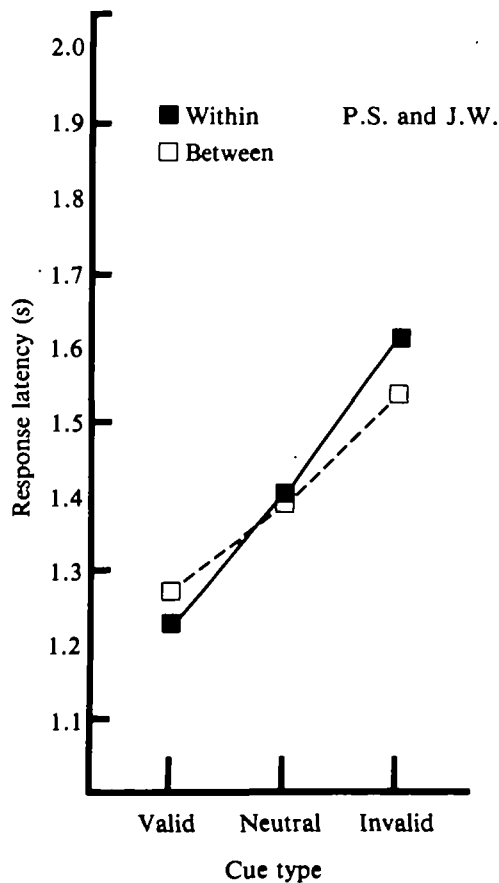


FIG. 2. Response latency as a function of spatial cue type. Data are presented separately for the Within-field Condition and the Between-field Condition. Each data point represents the average of two observers, with each given equal weight.

### *Experiment 2. Intra and Interfield Spatial Localization*

In order to assess the availability of visual information for explicit interfield comparisons, the same background configuration and temporal parameters were used to collect additional data in which an explicit comparison of two spatial positions was required. If the visual half-fields, which were previously integrated for the control of attention, proved to be disconnected for explicit stimulus localization, performance under within-field conditions would be expected to differ from performance under between-field conditions.

As in Experiment 1, fixation of the central spot was required throughout each trial. In the Within-field Condition, an 'X' appeared in one of the grid cells for 150 ms, followed 1.5 s later by another 150 ms presentation of an 'X', either within the same cell or in a different cell. In the Between-field Condition, the two 'X's appeared in homologous or different cells on different grids. The observer was instructed to respond 'same', by pressing the appropriate key, when the stimuli fell in the same or homologous cells, and, otherwise, to respond 'different'. The relative frequency of 'same' and 'different' trials in both conditions was 50 per cent.

### *Results and Discussion*

A total of 144 trials—2 blocks of 36 trials for each condition, alternated between hands and presented in a counterbalanced order—were collected from each of our observers, P.S. and J.W. An equal number of replications in each visual half-field were contained within each block of trials.

Observers' performance on the same/different task, expressed in terms of percentage correct, differed dramatically for our two conditions. In the Within-field Condition, P.S. and J.W. were accurate in their judgements on 83 and 93 per cent of the trials, respectively. This is comparable to their over-all performance on the odd/even judgements in our first experiment. In the Between-field Condition, however, performance fell to 64 correct and 56 per cent correct, respectively. Unlike the spatial priming effect obtained in Experiment 1, the difference between within-field performance and between-field performance on the same/different task was highly significant for each observer ( $P < 0.001$ ). This finding contrasts with that obtained for normal observers who have little difficulty with this task, and for whom the accuracy for both within-field and between-field trials is near-perfect.

Although observer P.S. was significantly impaired at between-field comparisons, it was somewhat surprising that his between-field performance was slightly better than chance ( $P < 0.05$ ). The reason for this is not clear. The recent evolution of interhemispheric transfer of phonetically-encodable stimulus information in this patient (Gazzaniga *et al.*, 1982) may have provided a basis for transfer in the present context. However, since, overall, P.S. was frequently incorrect in his judgements in the Between-field Condition, the occurrence of such transfer would be clearly insufficient to account for the similarity of within-field and between-field performance observed in the priming task.

J.W., on the other hand, is unable to transfer visual information of any kind for overt naming, and this observation is consistent with the finding that his performance at the interfield comparison task did not depart significantly from chance.

*The Resolution of Spatial Information for Attentional Control and Stimulus Localization*

The results of our two experiments imply that the commissurotomy patient has access to bilateral visual information that can be used to specify the locus of visual attention, but that is unavailable for explicit interfield visual comparisons. The following analyses were performed to examine the spatial resolution of visual information for attentional control, and to contrast the specificity of such information with that available for explicit interfield comparisons.

As noted above, the contrasting effects of the valid and invalid spatial cues in the priming task indicate that, when attention was directed across the visual midline, it was specific to the region of the cued target location. This finding implies that the effective locus of attention had a greater degree of specificity than the over-all size of the  $3 \times 3$  cell matrix within which the target appeared. It remains possible, however, that interfield spatial priming occurred both within the cued cell, as well as within cells which were nearby the cued target location. If so, response latencies on invalid cue trials would be expected to decrease as the relative proximity of the cued and actual target location increased. In order to explore this possibility, response latencies on invalid cue trials in which the target appeared in a cell adjacent to the cued cell were compared with those in which the cue and target appeared in relatively non-adjacent cells. Adjacent cells were defined as those abutting or immediately diagonal to the cued cell.

The results of these computations for both observers indicate that the priming effects in the Between-field Condition did not generalize to cells adjacent to the cued cell. For invalid cue trials in which the target appeared in a cell adjacent to the cued location, the mean response latencies for P.S. and J.W. were 1.45 s ( $N = 7$ ;  $SE = 0.14$  s) and 1.64 s ( $N = 7$ ;  $SE = 0.20$  s), respectively. These values contrast with average response latencies on valid cue trials for P.S. and J.W. of 1.29 s ( $N = 70$ ;  $SE = 0.03$  s) and 1.26 s ( $N = 67$ ;  $SE = 0.04$  s), respectively.

In addition, the average performance of our two observers was similar for targets appearing in cells adjacent and non-adjacent to the cued cell (average response latencies = 1.54 s and 1.50 s, respectively). When each observer is examined separately, however, the individual means for non-adjacent invalid trials are somewhat problematical. The average response latency on these trials for observer J.W. was 1.72 s ( $N = 7$ ;  $SE = 0.21$  s). This value is comparable to J.W.'s performance on adjacent invalid cue trials. On the other hand, the average response latency for P.S. on non-adjacent invalid cue trials, was 1.29 s ( $N = 7$ ;  $SE = 0.12$ ), which is identical to his performance on interfield valid cue trials. This finding, that response latencies decreased with increasing spatial disparity between the cued and actual target location, is opposite to what would be expected if the locus of priming generalized to neighbouring cells in the Between-field Condition. Rather, it may simply be a consequence of some combination of random variation, the relatively small samples which were available for these comparisons, and the smaller priming



effects, overall, for observer P.S. In sum, then, the above computations imply that the locus of attention in the Between-field Condition was specific to the cued cell.

Analysis of the results of Experiment 2, on the other hand, implies that, at least for observer J.W., bilateral spatial information was unavailable for explicit interfield comparisons, even in a crude form. An argument analogous to the one made above regarding the spatial priming effects that were obtained in Experiment 1 can also be made for the results of Experiment 2: if spatial information from both hemifields was available for the interfield comparison task, observers should have been most likely to erroneously equate the positions of stimuli which appeared in relatively adjacent cells. Stimuli appearing in relatively non-adjacent cells, which represented a spatial separation of at least 9 deg of visual angle, should have been easily distinguishable as appearing in different locations.

The results for observer J.W. indicate that this was not the case. The finding that his performance at the same/different task was not superior to chance is, of course, inconsistent with this interpretation. In addition, a comparison of J.W.'s performance on 'different' trials in which adjacent and non-adjacent cells were represented indicates that the relative proximity of the two 'X's did not systematically affect his performance. Thus, J.W. erroneously responded 'same' on 33 per cent (4/12) of the 'different' trials in which adjacent locations were represented; while he erroneously responded 'same' on 54 per cent (13/24) of those in which non-adjacent cells were represented. The difference between these values is non-significant ( $\chi^2 < 1$ ), and the tendency for adjacent locations to be less confused than non-adjacent ones is contrary to what would occur if crude bilateral spatial information was available for interfield comparisons.

As noted above, the performance of observer P.S. at the same/different task was superior to chance. In addition, despite having been informed that 'same' and 'different' trials were equiprobable, P.S. had a strong bias to respond 'different' in the Between-field Condition. Thus, while he was correct on only 44 per cent (16/36) of the 'same' trials in the Between-field Condition, he was correct on 83 per cent (30/36) of the 'different' trials. On 'different' trials, P.S. was incorrect on 33 per cent (4/12) of the trials in which relatively adjacent cells were represented and on only 8 per cent (2/24) of those in which non-adjacent cells were represented. The difference between these values is not significant ( $\chi^2 = 3.6$ ;  $P > 0.05$ ), but the trend is in the direction predicted if confusions between adjacent cells did occur. Thus, paracallosal interhemispheric transfer of a crude form of spatial information may have facilitated interfield comparisons for P.S. It is important to note that, whereas P.S. may have confused adjacent cells for explicit interfield comparisons, the effective locus of attention in the priming task appeared to be specific to the cued target location.

In sum, the over-all results of the above computations imply that the resolution of bilateral spatial information for the control of the locus of visual attention is superior to that available for explicit stimulus identification. It should be stressed,



however, that the dimension of the individual cells used in the present studies was quite large (4.5 deg of visual angle). It remains to be determined whether differences between within-field and between-field performance would emerge when finer spatial discriminations are required.

### GENERAL DISCUSSION

The results of these experiments imply that stimulus information as it exists for the explicit identification of spatial location can be distinguished from that used to direct the locus of visual attention. Several researchers have proposed that these functions are subserved by different anatomical pathways (Ingle, 1967; Trevarthen, 1968; Schneider, 1969). While their positions differ in detail, in general, it has been suggested that the primary geniculo-striate visual pathway plays a dominant role in the identification of visual stimulation, while the secondary colliculus-pulvinar-parietal visual pathway is concerned primarily with the allocation of visual attention.

To date, supportive evidence for the existence of two functionally and anatomically distinguishable visual systems in humans has derived exclusively from observations of residual function following lesion of a critical brain structure. It has been noted, for example, that, while damage to primary visual cortex results in visual field deficits (for instance, an inability to identify stimuli within the area of the scotoma), the patient is still capable of pointing to and foveating stimuli within the blind field (Weiskrantz, Warrington, Sanders and Marshall, 1974; Perenin and Jeannerod, 1975). On the other hand, studies of patients with damage to parietal cortex, and more recently the superior colliculus and pulvinar, reveal individuals with intact sensory capacities but a constellation of attentional deficits in response to contralateral stimulation (Heywood and Ratcliff, 1975; Friedland and Weinstein, 1977; Zihl and Von Cramon, 1979). Whereas these observations have demonstrated that one visual function can be spared when the other is lost, the co-existence of two visual systems simultaneously subserving different visual functions has heretofore been unreported.

In addition, the assessment of attentional capacities in patients with parietal or occipital damage has typically focused on overt motor behaviours associated with changes in the locus of attention (for example, the presence or absence of elicited saccadic eye movements; reaching or pointing movements of the hand) rather than on attentional control *per se*. While visually-elicited motor behaviour depends on an observer's capacity to orient to visual stimulation, the absence of such behaviour does not necessarily imply a deficit in the antecedent attentional processes (Robinson, Goldberg and Stanton, 1978).

The present findings provide the first demonstration of two functional visual systems in patients with intact, albeit interhemispherically disconnected, parietal and occipital cortex, under conditions in which performance depended upon the observer's ability to direct attention within the sensory environment independent of

the capacity to execute specific motor acts. If the observed spatial priming effects reflect predominantly parietal involvement, as the existing clinical literature would suggest, the question then arises as to the source of ipsilateral visual representation in parietal cortex. Two possibilities exist in this regard: following callosal section, ipsilateral visual representation may be provided directly *via* collicular-cortical projections, or it may be provided indirectly *via* the intact anterior commissure. Neither potential source of ipsilateral representation can be ruled out at the present time.

These data also raise questions concerning the cortical lateralization of attentional control. The present data imply that each separated hemisphere is provided with bilateral visual representation for the allocation of attentional resources. It remains to be determined whether, following callosal section, the disconnected hemispheres subsequently work in phase in the control of attention, or whether attention is controlled by a dominant hemisphere.

### SUMMARY

Following complete midline section of the corpus callosum, each separated hemisphere is unable to explicitly localize visual information appearing in the ipsilateral visual half-field and thus projecting to the other half-brain. Two studies are reported which reveal that, while commissurotomy patients are impaired at explicit interfield comparisons, the attentional system has access to both visual half-fields, thereby allowing one hemisphere to direct attention to specific spatial loci in the ipsilateral visual half-field.

### ACKNOWLEDGEMENTS

Aided by USPHS grant No. 2 RO1 NS 15053-02, the Alfred P. Sloan Foundation and the McKnight Foundation. We are grateful to Drs H. A. Sedgwick, A. Arditi and L. Festinger for their critical comments on an earlier version of this manuscript.

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(Received December 16, 1980)