

MANIPULO-SPATIAL ASPECTS OF CEREBRAL LATERALIZATION: CLUES TO THE ORIGIN OF LATERALIZATION

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(Received 28 February 1977)

Abstract—The right hemisphere advantage for split-brain patients on a variety of spatial tasks (block design, cube drawing, wire figures, and fragmented stimuli) is found to be highly dependent upon the involvement of manual activities in the perception of spatial relationships or the production of spatial responses. The cerebral localization of the neural substrate of manipulo-spatial functions suggests why the hemispheres differ along the manipulo-spatial dimension. These observations, in conjunction with other clinical data, are suggestive of the origins of cerebral lateralization.

INTRODUCTION

SOME years ago, striking differences were observed in the way the left and right hemispheres of split-brain patients performed on various tasks [1]. The initial findings were confirmed and extended in other commissurotomed patients [2–14, 41], and these results, along with data from different subject populations [15–39, 51, 52, 56], have led to the view that each half-brain has evolved its own specialized cognitive style and mode of information processing [7, 40–45]. However, this interpretation of functional asymmetry between the human hemispheres assumes that major qualitative changes in brain organization, which are unparalleled in phyletic history, occurred with the ascent of man.

In the present report, we describe experiments conducted on a recent callosal-sectioned patient, P.S. The experiments involve a simple though important methodological change (elimination of hand use as either the mode of stimulus perception or response production) in the design of several classic experiments. Although these are but one-subject demonstrations, our general approach is to first show that P.S. performs like any other split-brain patient on classic tasks when the test is administered in the traditional manner. However, when the design is slightly changed, though the stimulus material is held constant, the striking left–right difference is eliminated. These simple controls, in conjunction with cytoarchitectural considerations to be described, suggest that left–right differences may be more attributable to localized differences in cerebral organization than to the overall cognitive style of the hemispheres.

CASE HISTORY

P.S. is a right-handed, 15-yr old male. He experienced a severe series of epileptic attacks around the age of two, with a left temporal seizure focus. Subsequently, he apparently developed normally until age 10, when the seizures recurred spontaneously, and became intractable. In January 1976, he underwent complete surgical section of the corpus callosum. A more complete medical history has been published

elsewhere [46]. Behavioral testing has demonstrated a complete breakdown in the interhemispheric transfer of visual and tactile information. Thus, information lateralized to the left visual field and left hand cannot be verbally described.

OBSERVATIONS: METHODS AND RESULTS

All tests were carried out between the second and fifth postoperative months. In particular, the block design, cube drawing, and wire figures tasks were administered during the second month, while the fragmented stimulus task was administered during the fifth. Specific procedural details are provided with each test.

Block design task

One of the clearest and most dramatic demonstrations of hemisphere asymmetry results from the administration of the block design task to split-brain patients [6]. On each trial, the patient is presented with four patterned cubes and a sample design, and is required to manually arrange the cubes to form the design. The performance of each hand is separately timed. The data resulting from the administration of this task to our patient are shown in Table 1. The left hand consistently constructed the design faster than the preferred right hand, suggesting a clear right hemisphere superiority, as previously reported [6]. The question remained, however, whether the left hemisphere deficit lies primarily in the realm of stimulus perception or response production.

Table 1. Performance of left and right hands on block design task

Design	Time (sec)	
	Left hand	Right hand
1.	11	18
2.	*	74†
3.	13	36
4.	12	69
5.	15	95†
6.	25	74‡

*Design not completed within time limit (120 sec).

†Subject gave up before end of time limit.

‡Correct design was constructed, but in wrong orientation.

The sample designs were tachistoscopically lateralized to the hemispheres and the patient was required to select the appropriate design after visually inspecting the three choices before him. The correct design was always selected, regardless of the hemisphere tested. Thus, both hemispheres seem capable of appreciating the visuo-spatial aspects of this task, with the right hemisphere excelling relative to the left mainly in constructing the perceived relationships by manipulating the items appropriately.

Cube drawing

The preceding finding is consistent with our clinical observations regarding another dramatic instance of hemisphere asymmetry. P.S. could draw a cube with either hand prior to surgery. Following commissurotomy, however, as shown in Fig. 1, the drawing produced by the preferred right hand lacked the spatial completeness of the cube produced by the left hand, thus confirming the classic hemisphere difference [4]. Yet, it is not clear whether the right hand deficit results because the left hemisphere does not appreciate the spatial features of a cube, or because it cannot draw a cube.

When the word "cube" was flashed to his left hemisphere, P.S. readily selected a match-stick model of a Necker cube and ignored a model of the cube that had been drawn by his right hand. While this result alone is not very significant, it is consistent with the recent finding that both hemispheres of split-brain patients have the capacity to appreciate the spatial relations of Euclidean geometry [13]. Taken together, these observations suggest that the left hemisphere can indeed apprehend the spatial features of a cube, but, as with the block design task, the left hemisphere has difficulty in representing spatiality using a manual or manipulative response.

Other classic split-brain experiments, which have not required a manipulative response as such, have also suggested that the capacity for spatial appreciation is special to the right hemisphere. However, the following observations suggest that even in these experiments, the right hemisphere advantage is closely tied to manipulative activities.

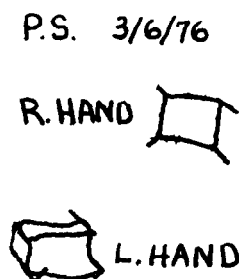


FIG. 1. Cubes drawn by the right and left hands.

Wire figures task

Milner and Taylor very convincingly demonstrated a right hemisphere advantage in the perception and memory of complex tactual patterns (wire figures) [12]. They suggested that this advantage represents the superior capacity of the right hemisphere for spatial processing, and thus should exist independent of the sensory modality tested.

We administered the wire figures task to our patient under four conditions. (The order of discussion represents the order of presentation of the conditions, and all conditions were administered on the same day.) In the tactual-tactual condition, the subject was required to palpate a figure with one hand and then immediately select the same figure from a group of four, using the same hand. In this condition, the left hand correctly retrieved all four figures, but the right hand performed at chance (one of four correct). This finding confirms the results of Milner and Taylor. The remaining conditions, which were not reported on by Milner and Taylor, were administered to test the generality of the right hemisphere advantage. In the tactual-visual condition, the subject palpated one figure and then pointed, with the same hand, to the sketch that matched the palpated figure. Neither hand erred. In the visual-tactual and visual-visual conditions, sketches of the figures were tachistoscopically lateralized and the subject was required to either tactually retrieve the figure or point to the figure following visual inspection of the choices. In these latter two conditions, both hemispheres again performed perfectly. Thus, when the manipulative system is either excluded from the wire figures task, or is augmented by adding a visual component to the match-to-sample design, the classic left-right dichotomy found for the manipulative (tactual-tactual) condition disappears. It is unlikely that this result is accountable for by a practice effect: Milner and Taylor found that the right hand of split patients, even with considerable training, generally failed to perform above chance in the tactual-tactual condition.

Fragmented figures task

Nebes found that the right hemisphere of split-brain patients was vastly superior to the left on a task designed to measure the capacity of the separated hemispheres to synthetically process spatial information [9]. The patients were required to manually examine three geometric designs while looking at a sketch of one of the items in a fragmented form. The fragment was constructed by cutting up and separating one of the designs, maintaining, however, the original orientation and relative position of the parts. The subject's task was to determine which one of the three items being tactually examined matched the fragmented stimulus. The right hand essentially performed at chance (33%), while the left hand scores ranged between 75 and 90% correct.

We altered the design of this experiment so that the synthetic demands of the task would be emphasized, as opposed to the manipulative demands. P.S. visually examined three fragmented forms on each trial. (The fragments were constructed in the manner described by Nebes.) Subsequently, a whole form, which matched one of the fragments, was tachistoscopically lateralized to the left or right hemisphere. Each hemisphere received 20 trials. Under these conditions, the left hemisphere correctly identified the fragment which the lateralized whole stimulus represented on 17 of 20 trials (85%), and the right hemisphere was correct on 20 of 20 trials. Thus, when the manipulative aspects of the figural unification task were eliminated and the synthetic processing demands were emphasized, both hemispheres proved capable of high level performance.

DISCUSSION

These experiments suggest that functional asymmetry between the hemispheres of split-brain patients on a variety of spatial tasks is highly dependent upon the involvement of manual activities. The importance of this point is highlighted by the fact that nearly every

instance of a right hemisphere advantage in split-brain patients has involved the hands as either the mode of stimulus perception [7–9, 11–13] or response production [4, 6].

The manipulo-spatial superiority of the right hemisphere is not attributable to a superior capacity for manual dexterity. It is, after all, the preferred right hand that lacks manipulo-spatial skills in the split-brain patient. Instead, we feel that the manipulo-spatial function is neither motor nor perceptual, *per se*, but rather is more appropriately viewed as the mechanism by which a spatial context is mapped onto the perceptual and motor activities of the hands. This mechanism is hypothesized to be part of the more basic mechanism by which the organism maintains an awareness of and appreciates the relationship between its body and the spatial environment.

It is interesting that although the left hemisphere of split-brain patients performs poorly on manipulo-spatial tasks, left brain damage produces deficits on some of the same tasks [15, 18–20, 23, 24, 26, 27]. In these studies, however, the right hand alone was usually tested, regardless of the hemispheric locus of the lesion. Had the left hand of left lesioned patients been tested, it seems less likely that a deficit would have been observed. We thus feel that the left hemisphere syndrome may go beyond a simple lesion effect and instead the lesion may serve to disconnect the motor regions of the left hemisphere that control the right hand from the manipulo-spatial mechanisms of the right hemisphere.

Clinical data from brain-damaged humans indicate that the neural substrate of manipulo-spatial and other functions involving the relationship between the body and space is contained in the inferior parietal lobule and parts of the remaining parieto-temporal function [18–20, 23, 24]. However, these data point out that, in man, the right parieto-temporal junction plays a greater role in spatial activities than the homologous area in the left hemisphere. This is understandable, for the entire parieto-temporal region in the right hemisphere is potentially available for the mediation of manipulative and other spatial activities, but extensive language functions occupy the left parieto-temporal junction [49]. In contrast, experimental work on non-human primates indicates that cell populations in the inferior parietal lobule of both hemispheres contribute to the mediation of manipulative behavior in extrapersonal space by providing the organism with an awareness of the relationship of his bodily parts to their spatial environment [47, 48].

These comparative observations suggest to us that with the evolution of man and the emergence of language, synaptic space devoted to body-space functions in the left hemisphere of preverbal primates was sacrificed. As a consequence, we feel that the superior performance of the right hemisphere of split-brain patients on a variety of manipulo-spatial tasks may not reflect the overall cognitive style and evolutionary specialization of the right hemisphere, but instead may represent localized processing inefficiencies in the left parieto-temporal junction due to the presence of language.

The overall explanatory value of this hypothesis concerning the origins of cerebral lateralization is emphasized by the fact that, as we have noted, nearly every demonstration of right hemisphere dominance in split-brain patients has involved manipulo-spatial activities [4, 6–9, 11–13]. The major exception to this is Levy, Trevarthen and Sperry's demonstration of right dominance on the bilateral chimeric stimulus task for split-brain patients tested several years postoperatively [14]. When chimeric tests were administered to P.S. at various postoperative sampling points, beginning one month after surgery, we found that right dominance gradually emerged to replace bilateral responding with increasing postoperative time [50]. This suggests the possibility that right dominance on the chimeric task may be a developmental consequence of learning to live with two independent

half-brains. Furthermore, as Levy *et al.* noted, right dominance simply involves control over the response mechanisms, for both half-brains form visual percepts. Also, there are methodological problems with Levy *et al.*'s conclusion that the hemispheres used different cognitive strategies in forming their percepts. First, although the patients gave analytic descriptions of "non-verbal" stimuli presented to the left hemisphere, verbal descriptions are by their very nature analytic. So, even if the left hemisphere fully perceived the non-verbal stimuli, its verbal description of such stimuli would necessarily be piecemeal. Second, while the left hemisphere accrued more errors on non-verbal chimeric tests than did the right, this effect may be attributable, at least in part, to the fact that the left hemisphere task (naming and/or describing) was more difficult than the task required of the right (pointing).

Although normal studies of perceptual asymmetry [38, 39, 51, 52, 56] do, in fact, suggest a right hemisphere advantage on certain "non-verbal" tests, the hemisphere differences, when found, are generally small and statistical, and thus fail to replicate the dramatic, qualitative differences observed when manipulo-spatial tasks are administered to split-brain patients. Also, studies of visual perception following lateralized brain damage suggest that while the right hemisphere does seem to have a perceptual advantage, the effect mainly surfaces when the tasks tax the discriminative and integrative capacities of the hemispheres [36, 53-55]. Furthermore, a simple extension of the notion put forward earlier accounts for these normal and clinical observations. To the extent that language uses up space in the left hemisphere, non-language functions must operate in less space. It is not that the left hemisphere completely lacks non-verbal perceptual functions, it simply has a lesser representation of these functions. As a consequence, relative to the left hemisphere, the right has an advantage, particularly when the upper limits of the functions are tested.

Thus, while studies of split-brain, normal, and brain-damaged subjects clearly demonstrate that functional asymmetry is a salient feature of human brain organization, these studies also demonstrate that there are inherent similarities in the types of processing that occur in the left and right half-brains. In addition, the results of these various studies do not necessarily lead to the conclusion that what is lateralized in the human brain is the wholistic vs the analytic mode of information processing. Finally, the data suggest the possibility that many of the differences that do exist between the human hemispheres may be more attributable to localized differences in processing that are closely tied to the inter- and intra-hemispheric localization of language than to the evolutionary specification of cognitive style.

Acknowledgements—Special thanks to Dr. GAIL RISSE. Work supported by USPHS Grant No. 25643.

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Résumé :

On a trouvé que l'avantage de l'hémisphère droit pour les sujets split-brain sur un nombre d'épreuves spatiales (arrangement de blocs, dessins de cubes, formes sans signification et stimulus fragmentés) dépend considérablement de l'implication des activités manuelles dans la perception des relations spatiales ou la production des réponses spatiales. En raison de la localisation cérébrale du substrat nerveux des fonctions manipulo-spatiales, on peut comprendre pourquoi les hémisphères diffèrent selon la dimension manipulo-spatiale. Ces observations ajoutées à d'autres données cliniques fournissent quelques suggestions sur les origines de la latéralisation cérébrale.

Deutschsprachige Zusammenfassung:

Bei Patienten mit durchtrenntem Balken zeigt sich die rechts-hemisphärische Überlegenheit bei einer Anzahl von Raum-Aufgaben (Mosaik-Test, Würfel Zeichnen, Drahtbiegeprobe und unzusammenhängende Stimuli) in deutlicher Abhängigkeit von der manuellen Beteiligung bei der Perzeption von räumlichen Beziehungen und von der Produktion an "Raum-Antworten". Die cerebrale Lokalisation des neuralen Substrates von Leistungen, die räumliches Handeln erfordern, erklärt, warum die Hemisphären sich in der Hand-Raum-Deminsion unterscheiden. Diese Beobachtungen, in Verbindungen mit anderen klinischen Daten, deuten auf den Ursprung cerebraler Lateralisation hin.