1972

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[*Reprinted from* BRAIN, *Vol. 95, Part I, 1972, pp. 61–78*]

MACMILLAN JOURNALS LIMITED
LITTLE ESSEX STREET, LONDON

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1972

Brain (1972) **95**, 61–78.

PERCEPTION OF BILATERAL CHIMERIC FIGURES FOLLOWING HEMISPHERIC DECONNEXION

BY

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(*From the California Institute of Technology*)

PATIENTS who have undergone surgical section of the fore-brain commissures for control of intractable epilepsy (Bogen and Vogel, 1962, 1963; Bogen, Fisher and Vogel, 1965; Bogen, Sperry and Vogel, 1969) retain mental function in each of the disconnected hemispheres. These, and especially those with little additional cerebral damage, offer special advantages in studying cerebral dominance and the lateral specialization of cerebral function. Strong lateralization of speech and calculation to the disconnected left hemisphere in right handers, and a specialization of the disconnected right hemisphere for visuo-spatial construction in them is generally confirmed (Sperry, Gazzaniga and Bogen, 1969; Bogen and Gazzaniga, 1965). Superiority of the minor hemisphere has also been demonstrated for visuo-tactile transformation from two to three dimensions (Levy, 1970; Levy-Agresti and Sperry, 1968), for perceptual identification of complete circles from knowledge of circle segments (Nebes, 1971), and for perceptual completion of visual half-figures fragmented at the vertical meridian (Trevarthen and Kinsbourne, 1972). These findings on lateralization of cerebral function after commissurotomy conform with and strengthen deductions drawn from studies on the effects of unilateral cerebral damage (Lerbert, 1965; Hécaen, 1962) as well as from studies on left-right field differences in perception with normals (White, 1969).

Recent commissurotomy studies have also shown that the two disconnected hemispheres, working on the same test task, may process the same sensory information in distinctly different ways, and that the two modes of mental operation, involving spatial synthesis for the right hemisphere and temporal analysis for the left, show indications of mutual antagonism (Levy, 1970). The propensity of the

Supported by the Frank P. Hixon Fund of the California Institute of Technology and by U.S. Public Health Service Grants No. MH 03372 and No. MH 46980-01. The subjects examined were patients of Drs. Philip Vogel of the California College of Medicine and Joseph Bogen of the Ross Loos Medical Group, Los Angeles.

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language hemisphere to note analytical details in a way that facilitates their description in language seems to interfere with the perception of an over-all Gestalt, leaving the left hemisphere "unable to see the wood for the trees." This interference effect suggested a rationale for the evolution of lateral specialization and led to a prediction, partially confirmed (Silverman *et al.*, 1966; James *et al.*, 1967; Levy, 1969; Miller, 1971), that bilateral language competency, as found statistically among left handers, should produce a correlated perceptual-performance deficit.

In the present study lateral specialization of the hemispheres is examined further with a different testing technique which uses the tendency of each hemisphere to effect perceptual completion of patterns beyond the vertical mid-line (Trevarthen and Kinsbourne, 1972). The method gives a direct comparison of the ability of each hemisphere to separately perceive and respond to stimulus patterns, as well as a comparison of their respective capacities to exercise a dominating control over the motor response according to the testing conditions. The results present evidence for a specific functional superiority of the right hemisphere for tasks involving recognition and comparison of visual form and also demonstrate the capacity of the disconnected "minor" hemisphere to dominate the motor performance for certain mental activities.

METHOD

Subjects

Tests were conducted during April to August 1970 on four of the patients of Drs. P. J. Vogel and J. E. Bogen (N. G., L. B., A. A., and C. C.) all of whom had undergone surgical section of the fore-brain commissures including the entire corpus callosum and the anterior commissure. The hippocampal commissure was presumed to have been sectioned along with the callosum; the massa intermedia was also divided where it was seen to be present (Bogen and Vogel, 1962, 1963; Bogen, Fisher and Vogel, 1965; Bogen, Sperry and Vogel, 1969). These four were selected from a population of seven available commissurotomy patients because they were thought to have least asymmetrical cerebral damage of a kind that might affect higher psychological functions.

N. G. had been operated on in September 1963 at age 30, and was living a basically normal life as a housewife. Before operation there was radiological evidence of a 2 cm calcification in the central part of the Rolandic fissure of the right hemisphere, and EEG signs of abnormality in the posterior temporal lobe of the left hemisphere. Generalized or temporal lobe seizures began at age 18. A more detailed medical report is given in Bogen, Fisher and Vogel (1965). Her post-surgical scores on the WAIS (Wechsler Adult Intelligence Scale), administered in August 1968, were 83 verbal and 71 performance. She is right-handed, of a right-handed family.

L. B. was a 17-year-old schoolboy at the time of testing. Aside from the seizure history since age 3, there were no distinct X-ray or other signs of brain damage in either hemisphere at the time of operation at age 13. He is right-handed. He has a tendency to aberration of convergence with monocular diplopia of the left eye, a familial trait also present in his father. His post-surgical WAIS scores at age 16 were 110 verbal and 100 performance.

A. A. was operated upon in 1964 and when aged 19 was enrolled in a special programme for the handicapped at a city college. He has damage from a presumed birth injury in the fronto-parietal area in a region extending dorsal from the Sylvian fissure in the left hemisphere. His seizures, which started at age 5, were manifest as focal motor activity on the right side. Correlated with this, his touch sensibility in the right hand is markedly reduced. Since operation he drags his left leg when walking, the onset being when he had œdema and intracranial pressure during surgical recovery, with indications of frontal damage in the right hemisphere. He is slow of speech and performs tests of verbal facility and calculation poorly. His WAIS I.Q., four years after surgery, was 77 verbal and 82 performance. A general case study of this patient is provided in Nebes, Bogen and Sperry (1969).

C. C. is an 18-year-old boy in a special home for the handicapped. When 8 he began to show personality changes, having fights and falling behind in school. When 10 his family noticed periods of speechlessness, with turning of the head to the right, occasional falls, and loss of consciousness. The frequency and severity of seizures and antisocial behaviour progressed up until the time of operation when he was 13. The EEG showed a lesion in the temporo-parietal area of the left hemisphere. On the WAIS he scored 72 verbal and 75 performance at three years after operation.

All of these patients have been extensively tested in psychological and neurological studies throughout the post-operative period. In all four cases the seizures have been well controlled with light medication since surgery, N. G. having been entirely seizure-free for more than seven years. Normal controls were drawn from laboratory staff and acquaintances, all with at least high school education.

Apparatus and Stimuli

A modified Harvard two-channel tachistoscope, Gerbrands model No. T-2B-1, was used for stimulus presentation (fig. 1A). The stimuli as described below were presented on small cards seen by the subject as white squares subtending 5 degrees of visual angle centred on the fixation point. These cards were supported in a black velvet, non-reflecting background into which they were inserted from behind, and viewed through the half-reflecting mirror. The fixation field was provided by a panel of translucent indigo blue plastic, illuminated uniformly and continuously from behind with white light at 0·2 Ft. L. In the centre of the field, which measured 20 degrees × 20 degrees, was a bright red spot of light five minutes of arc in diameter that served as the fixation point. When illuminated, the stimulus card had a luminance of 2·5 Ft. L. It was seen to appear and disappear against the unchanging blue background. The testing room was diffusely illuminated from ceiling lights reduced to give a table-top illumination of 4 Ft. Cd.

The stimulus was presented for 150 msec., which was too quick for a reflexive eye movement to shift fixation to a new point. The subject was given the signal "ready," indicating that he should fixate on the red dot, 0·5 to 1·0 second prior to stimulus onset. In addition, eye movements were recorded by means of two non-polarizing electrodes placed just lateral to each eye with a third "ground" electrode on the forehead. A continuous readout of the D. C. electro-oculogram was obtained on a Beckman Type R Dynograph and sections of the record were simultaneously displayed on Tektronix Model 564B storage oscilloscope. A light, elastic "hat" band was fitted to the subject's head, connected to a counterweighted, low torque potentiometer, for recording horizontal head rotations. With this technique, which is described in detail elsewhere (Trevarthen and Tursky, 1969; Trevarthen and Sperry, 1972), eye movements were measured to an accuracy of 1 degree of arc. The examiner monitored stimulus artifact, E.O.G., and the subjects' vocal responses on the storage oscilloscope with a 5 cm/sec sweep initiated at the ready signal. The onset button of the tachistoscope was activated only if the eye movement tracing showed *S*'s gaze to be fixed on the red dot. Fig. 1B shows an example of the record from the oscilloscope.

The tests were monocular, using the patient's dominant eye as determined by preliminary tests in which interocular conflicting stimuli were presented to the two eyes by means of polarizing filters. L. B. and N. G. were strongly right-eye dominant. C. C. had mixed dominance, but was more attentive to the right eye, and A. A. was left-eye dominant. Extra trials with the non-dominant eye gave the same results; the dominant eye was used for optimal vision.

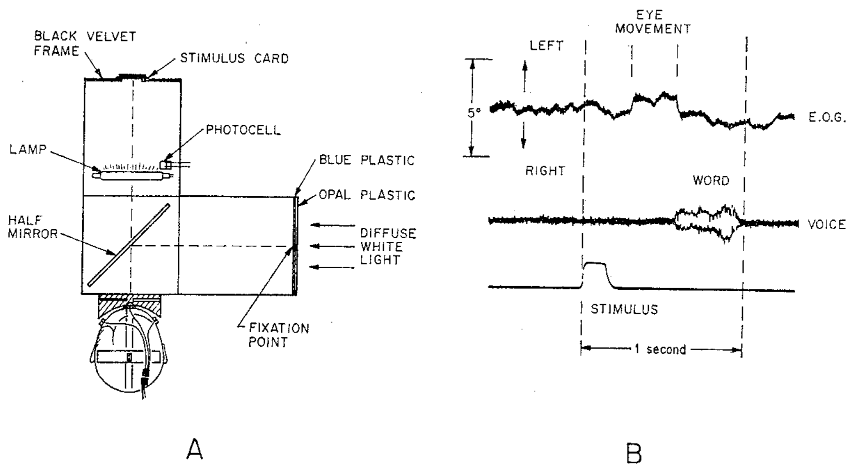

FIG. 1.—A, Tachistoscope with constantly illuminated fixation field. Subject with E.O.G. electrodes and attachments for head recorder. B, Sample tracings from the storage oscilloscope of E.O.G., microphone and the photometer recording stimulus artifact. The small eye movement, latency 250 msec, is of a size appropriate to inspection of an eidetic store of the left half of a chimeric stimulus.

Tests of different perceptual functions were designed from (*a*) photographs of faces, (*b*) ambiguous solid black figures resembling antlers, (*c*) line drawings of familiar items and (*d*) three-item patterns of squares and crosses in a vertical row (*see* figs. 3–7). The chimeric stimulus presented in the tachistoscope consisted of the left half of one stimulus figure joined at the mid-line to the right half of another stimulus figure. For faces 1, 2 and 3, for example, the tachistoscopic stimuli were the six combinations, 1-2, 2-1, 1-3, 3-1, 2-3, and 3-2, the number on the left representing the left-field face, and the number on the right, the right-field face (fig. 3). For visual matching, the original three whole stimuli were presented in free vision on the table in front of the subject and the subject was instructed to choose on each trial by pointing to the one he had seen flashed in the tachistoscope. In naming tests no whole stimuli were visible; the subject simply said what he had seen. The procedure was identical for the antler, familiar object, and chain-pattern tests, except that in the latter case (*see* fig. 7) there were 8 base stimuli instead of 3. These 8 stimuli consisted of all possible permutations of squares and crosses which could be arranged in a vertical sequence of 3. The chimeric arrangements for these 8 stimuli were 32 in number, such that if there were two or three squares on one side there was only one square on the other side, and similarly for crosses.

Experimental Plan and Procedure

Chimeric stimuli of the kind shown in figs. 3–7 were presented centrally in the subject's visual field with the aim of inducing separate and rival perceptual processes in right and left hemispheres. The design of the tests depended upon the phenomenon of "hallucinated completions," i.e. the fact that commissurotomy patients, when confronted with a stimulus which extends across the mid-line of the visual field, will say that they see a whole and complete stimulus although a given hemisphere can see viridically only that part of the stimulus which is in the contralateral visual field (Trevarthen and Kinsbourne, 1972). Therefore, when a half stimulus is seen in the left field and a half of a different stimulus is seen in the right field, each hemisphere by completion perceives a different whole stimulus. Right and left inputs were balanced for over-all spatial and temporal properties, but contained distinctive differences so that the images perceived by the two hemispheres were in direct conflict. Various effects of this conflict were utilized to study different aspects of hemispheric specialization.

The subject looked into a tachistoscope and was told he would see a picture flashed briefly, and that he was then to point to the same picture among an array of 3 to 8 similar pictures or patterns arranged in easy view on the table before him. The tests involving chimeric faces were presented first to each subject, "antlers" second, line drawings of familiar objects third, and the chain patterns fourth. Each test was run on a different day. Three modes of response were required for each test. In the first, subjects responded by pointing to the choice stimuli with the right hand, in the second, by pointing with the left hand, and in the third we removed the choice stimuli, and the subject was requested to name what he had seen. Occasional double responses for both right and left stimuli (2·3 per cent of all trials) were not included in the reported scores. Further details specific to each test are given below in context.

OBSERVATIONS

I. Facial Recognition

Recognition of faces appears to be strongly gestalt-like in nature and a face is relatively resistant to analytical verbal description. Hécaen (1962) and Rondot and Tzavaras (1969) found that most patients with prosopagnosia have lesions of the right hemisphere. It was accordingly anticipated that appropriate tests might show the disconnected minor right hemisphere to be superior to the major in performing facial recognition. This was confirmed in our results which are tabulated in fig. 2 and which indicate clearly a strong asymmetry of function in favour of the minor hemisphere. All subjects showed a preference for the face presented on the left of the chimeric figure (fig. 3) and the error rate was low (3 per cent). Even when the right hand was used for pointing, face selection was controlled predominantly from the minor hemisphere. On rare occasional trials the right as well as left faces were correctly chosen; such double responses were not included in the histograms (fig. 2).

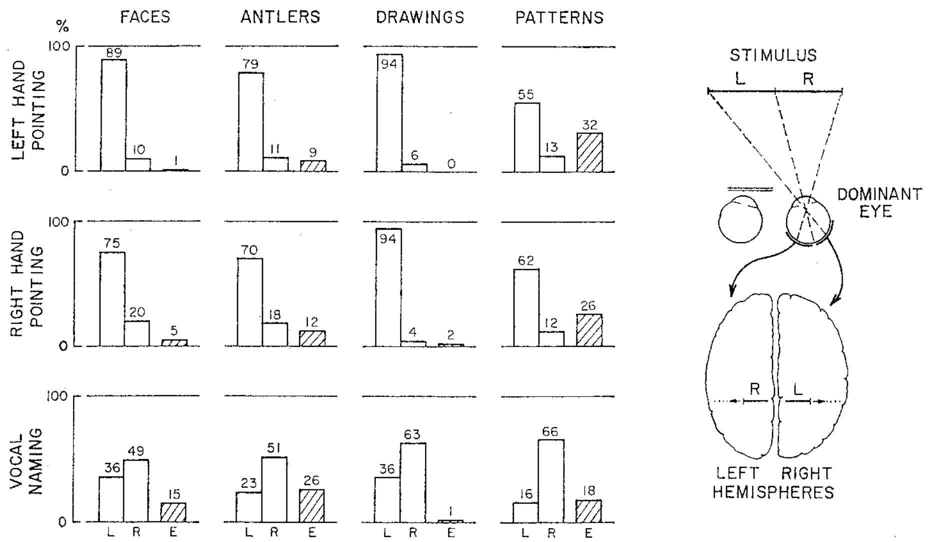

FIG. 2.—Summary of results: percentage choices favouring left (L), or right (R) halves of chimeric stimuli, and errors (E). Infrequent double responses (to both halves of a chimera) are excluded.

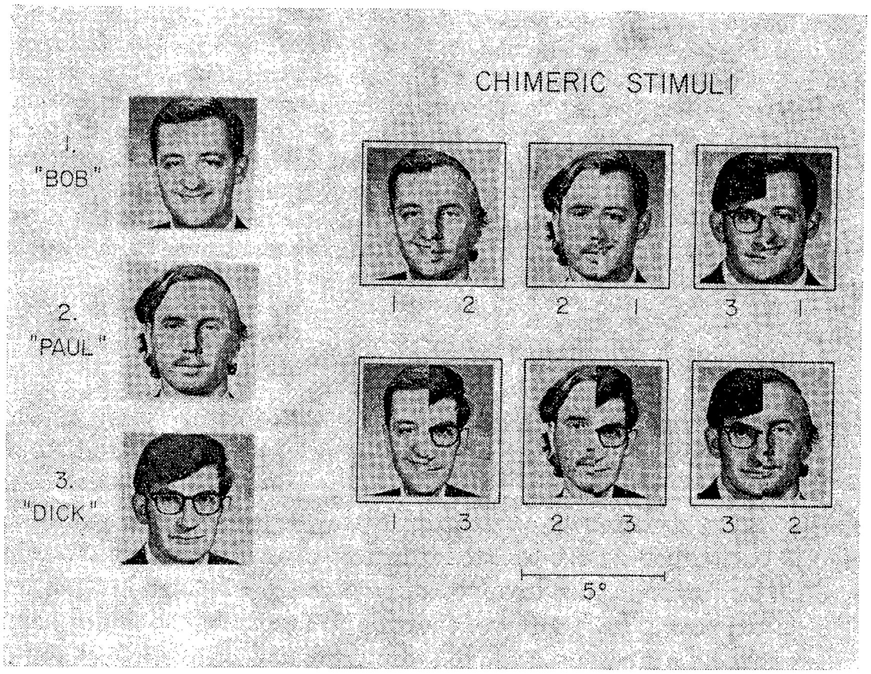

FIG. 3.—Test for recognition of faces.

In the third version of the test, in which the whole choice stimuli were removed and the subjects simply named the face seen, the subjects were taught in advance that face 1 was "Bob," face 2 was "Paul," and face 3 was "Dick." All four patients appeared to have unusual difficulty in learning these name associations, requiring 10 to 15 minutes to learn the names, succeeding eventually only by assigning some verbal label to a distinctive feature of each face, saying such things as "Dick has glasses, Paul has a moustache and Bob has nothing." Controls by contrast could retain the names after having stated them but once.

When we switched to a response by verbal naming instead of manual matching the scores abruptly reversed in favour of the right half of the chimeric stimulus (49 per cent versus 36 per cent). The percentage of errors increased from an average of about 3 per cent with pointing read-out to 15 per cent with verbal read-out (a difference in error rate significant at better than the ·001 level). Even so, non-error responses account for 85 per cent of the total, indicating that even with verbal read-out, the subjects were significantly better than chance. It was evident in the hesitancy and incidental comments of the subjects as well, that the left hemisphere found this kind of task extremely difficult and was inclined to describe the distinctive features of the right field face instead of naming it as a unit.

To check this indication that recognition of unfamiliar faces as a whole is especially difficult for the left hemisphere, a further series of trials was run using the same procedure except that the whole faces were exposed in the right field for identification by pointing with the right hand. From subject's scores, response latencies and behaviour it was clear that the performance by immediate recognition was markedly inferior to that mediated by the right hemisphere in the preceding sessions.

Questioning of the patients after completion of the facial recognition series showed that they apparently had no awareness whatever that the chimeric tachistoscopic stimuli were in any way conflicting or incomplete. They insisted that the face seen in the tachistoscope was like one of the choice stimuli. Even leading questions such as, "Did you notice anything at all peculiar about what you just saw?" failed to elicit any indication that the subjects were aware of having seen split and recombined faces. Normal controls on the other hand detected immediately or after the first few trials, that the faces were combinations of two different half-faces.

Tests for bilateral images.—The foregoing could be interpreted to mean that each chimeric stimulus typically led on each trial to the formation of two separate perceptual images, one in each hemisphere, only one of which then gained overt expression depending on the conditions of the test task. This interpretation was favoured by occasional double correct responses with pointing which seemed to reflect the presence of 2 percepts in some trials, at least, but there were only 6 such double responses in 252 trials with chimeric faces. The existence of the second unexpressed percept in the majority of trials remained in question and alternative interpretations in terms of some kind of obligatory reciprocal suppression or lateralized neglect remained possible.

Accordingly an additional set of trials was run to test more specifically for the presence of the subordinate percept by blocking the routine response which the subject was prepared to make and requesting a different kind of response to favour the opposite hemisphere. For example, the subject was instructed, before stimulus presentation, to point to the matching face but before he could start to respond the face array was temporarily removed and he was asked instead to first tell the examiner what had been seen and only later was asked to point. On other trials the subject was instructed to describe the stimulus but before starting was interrupted and told to first point to the correct face. "Interrupted" trials of this kind were interspersed among regular trials in which the instructions were not reversed. A new and unfamiliar set of faces was used with an array of 8 instead of 3 for the subject to choose from as shown in fig. 4.

The results with the 2 subjects who were given this test (N. G. and L. B.) clearly indicated the presence in six of eight trials of two separate percepts both of which were correctly designated by a combination of manual and verbal response. Consistent with the earlier results the manual responses were directed to a match for the left half of the stimulus and the verbal responses described the right half. In these double responses, the conflict between the verbal and the manual responses became evident to the subjects and resulted in a considerable perplexity and confusion. This was lessened by both the brevity and the incompleteness of the exposure which tended to leave a somewhat uncertain impression of each stimulus half. When the verbal response came first under direction from the left hemisphere the right hemisphere had to choose between the announced verbal selection and its own strong impression favouring another of the faces. In only one trial in four did this result in loss of the response preferred by the right hemisphere. When the manual response came first the verbal hemisphere had to decide whether to be consistent and describe the

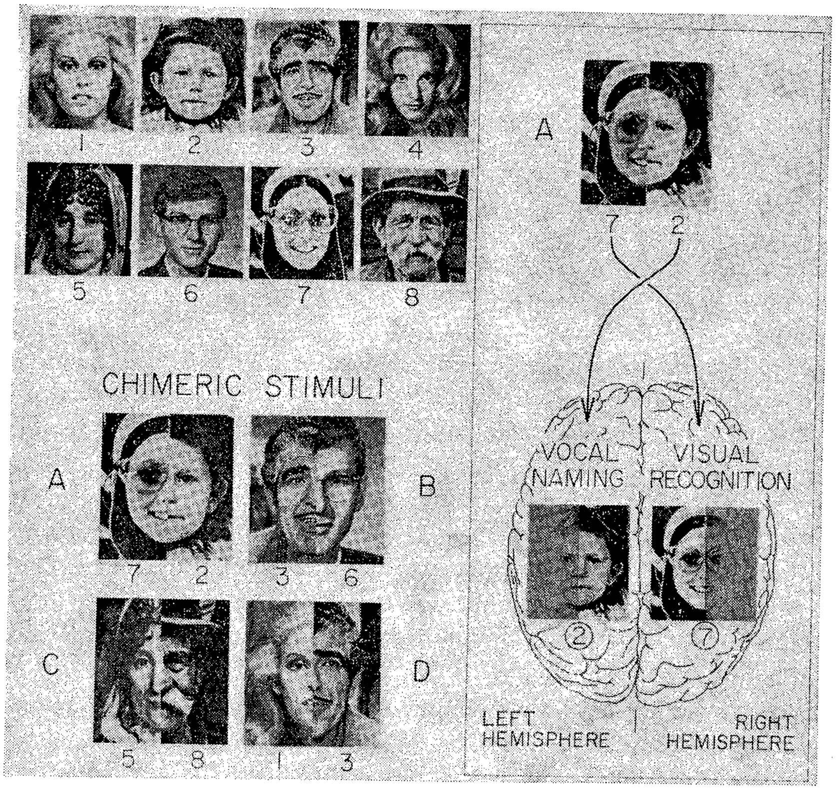

FIG. 4.—Additional test for simultaneous perception of faces by the two hemispheres. On right: diagram of projection of a chimeric stimulus to both halves of the brain to produce two complete dual different percepts.

face that had already been pointed to or to ignore this in favour of its own recall of a different face. Again, omission of all reference to the second (right half) face occurred only once in four trials. Among the variety of possible choices under these conditions both subjects consistently confined their responses to the two faces represented in the stimulus in each trial.

II. Apprehension of Nameless Forms

A second set of tests was concerned with the question of whether the minor hemisphere's special ability to recognize faces is specific, or reflects a more general capacity of this hemisphere for apprehending complex spatial forms. The former alternative is suggested in observations of infants (Wolff, 1963), normal adults (Yin, 1969), and in the brain damaged (Yin, 1970; Tzavaras, Hécaen, and Le Bras, 1970). In designing the present test the aim was to create stimuli that had properties, like bisymmetry and complex organization, in common with faces but at the same time were not face-like, were unfamiliar and were not readily distinguished by name or by subsidiary features.

The scores obtained with the "antler" patterns (fig. 5) were comparable in most respects to those of the face test. They similarly showed a strong preference, in favour of the left field for manual pointing by either hand and a sharp reversal in field preference and increase in error rate with verbal read-out (fig. 2).

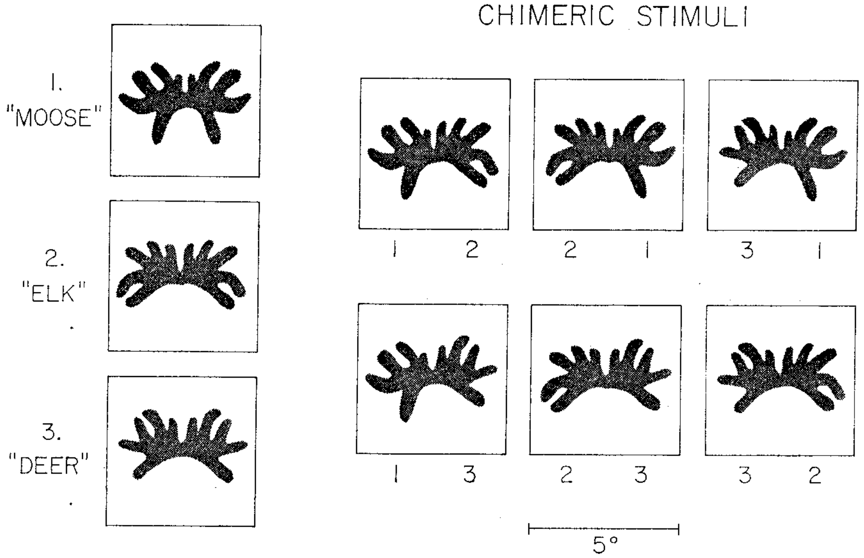

FIG. 5.—Perception of unfamiliar forms.

For verbal naming the subjects were taught in advance while viewing the whole stimuli that "antler 1" was that of a "moose," "antler 2" an "elk," and "antler 3" a "deer." As with faces, the subjects had abnormal difficulty in associating and retaining correctly the assigned names. This was not, at first, facilitated to any significant degree by advising them to consciously search for verbal criteria. N. G. was asked to name the antlers after repeating her own descriptions of the characteristic differences (i.e. large = "moose," bent = "elk," small = "deer") with no significant effect on her score. L. B., however, learned to single out and use distinctions among the most lateral branches on the right side.

N. G. was also tested with whole antlers 1, 2 or 3 projected entirely within the left or right visual field. The 5 degree pictures were centred at 3 degree left or right of the fixation point and 27 trials were given in each half-field, in two separate runs with the left hand being used to match left field stimuli and the right hand for right field stimuli. N. G. was more accurate for left field than for right field stimuli (left = 92 per cent correct, right = 60 per cent correct). Her left field responses were more automatic and appeared to come quickly, without thinking. With right field pictures there was more hesitancy. As N. G. expressed it, "she felt less sure," and had to "go over it in her mind . . . to see which piece was larger or smaller." Again the results suggested that this type of task is more difficult for the major hemisphere, whether or not a conflicting stimulus is present in the opposite hemisphere.

The higher over-all error rate obtained in the antler test can be correlated with the fact that these forms were more difficult than were the faces both to distinguish and also to analyse. Despite the increase in double responses in which the subject deliberately indicated both halves of the chimeric stimuli by pointing twice with a responding hand, no subject reported verbally having seen asymmetric or double stimuli. Normal control subjects, after perceiving that the stimuli were chimerical combinations, were able with effort to retrieve both halves of the stimuli in a majority of trials, by employing conscious strategies with voluntary control of orientation to left and right halves.

The antler test to the right half-field was also run on a hemispherectomy patient (G. E.) who had undergone removal of the minor right hemisphere for a malignancy four years previously at age 28. The absence of the right hemisphere might be expected to cause a selective handicap for this task. Pointing with the non-paralysed right hand, she correctly matched the exposed form in 21 out of 24 trials. In verbal naming she was correct on the first nine consecutive trials then broke down to a chance level. This inability to sustain a mental task was characteristic of her post-operative behaviour as was also a predominant superficial vocality and hyperreactivity to vocal stimuli. Her performance with the remaining left hemisphere falls into the upper performance range of the left hemisphere of the commissurotomy patients.

III. Recognition of Highly Familiar Objects

The stimuli employed in the third test differed from the preceding in that the forms represented in drawings (fig. 6) were highly familiar to all subjects from early childhood. We were interested to know whether we would still find the same minor hemisphere superiority for the recognition of common objects with well-known and long-established verbal labels. The particular items used were chosen to have monosyllabic names with different vowels for subsequent use in a test of the abilities of left and right hemispheres to perform rhyming (*see* Levy, Trevarthen and Sperry, 1972). The results proved to be basically in line with those obtained for faces and unfamiliar forms. A strong left field preference was obtained in the trials involving selection by manual pointing with either left or right hand. The reversal of field preference from left to right that occurred when the response was shifted from manual read-out to vocal naming was especially strong in this test; 63 per cent right field responses were given with vocal naming, and 4 per cent with right hand pointing.

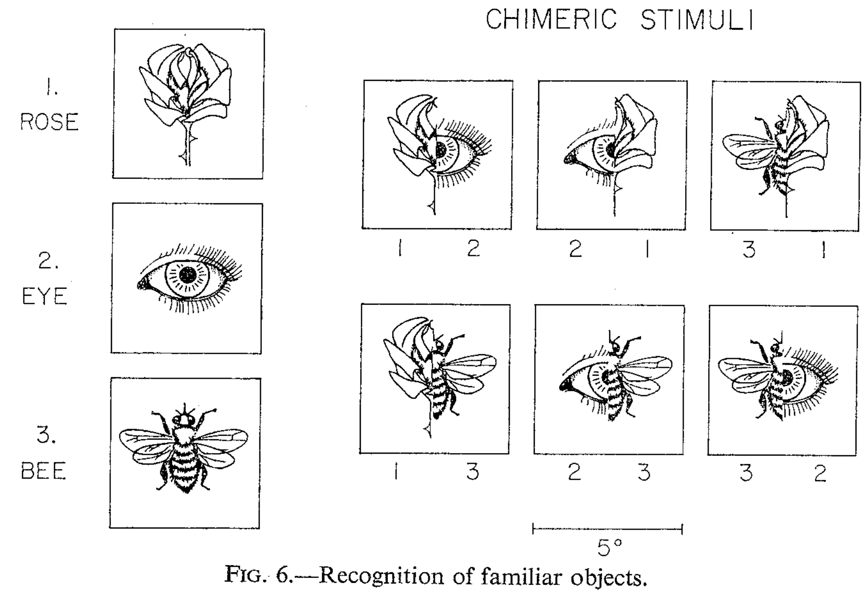

FIG. 6.—Recognition of familiar objects.

An exception to this was obtained in one testing session with L. B. in which he correctly named the left half of the stimulus in 23 out of 24 trials. His responses in this run were slow and stereotyped.

He complained about their difficulty and closed his eyes after each stimulus presentation as if to better concentrate on a retained visual image. This exceptional run is of special interest in its suggestion of minor hemisphere speech, sporadic indications of which were seen elsewhere in this subject and more clearly in A. A. Alternative interpretations that are not excluded include speech from the left hemisphere about ipsilateral half-field information mediated through the brain-stem (Trevarthen and Sperry, 1972), or combined use of left and right halves of the brain in speech as discussed in a forthcoming report on responses to coloured chimeric patterns (Trevarthen, Levy and Sperry, 1972*a*).

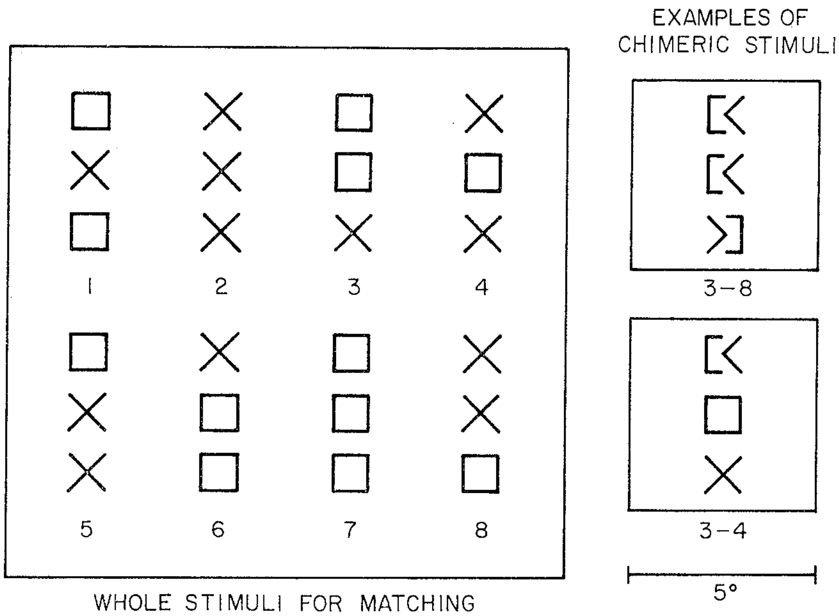

FIG. 7.—Stimuli for the chain pattern test.

IV. Chain Patterns

The chain pattern test (fig. 7) was included because, unlike the unified stimuli of the preceding tests, patterns of this kind lend themselves to a piecemeal, sequential analysis, that might be expected to favour the major hemisphere (Paterson and Zangwill, 1944). In this test both hemispheres saw the identical elements on each exposure but permuted in different ways on the two sides. The results for direct matching by manual signal were comparable to those from the other tests in showing a strong right hemisphere preference with either hand. The higher error rate on this test results from the use of 8 instead of 3 choice stimuli making chance error 75 per cent (because 2 out of the 8 alternatives will be correct by chance) instead of 33·3 per cent. In order to compare proportions of correct responses due to non-chance factors (P_K) for a test with 8 versus 3 alternatives, we used the following equation:

$$P_A = P_K + (1 - P_K)P_G$$

where P_A is the proportion of actual correct and P_G is the probability of being correct by chance. For the chain-pattern test $P_K = \cdot 6133$ and for the antler test it equals

·6847. Thus the minor hemisphere apparently found the recognition of the chain patterns to be of the same level of difficulty as the recognition of antlers, but the result was quite different for the major hemisphere and vocal read-out, where P_K for antlers was only ·2192, but was ·7600 for patterns. Apparently the major hemisphere as predicted found it much easier to identify chain patterns of this kind in verbal terms than it had the antler-like patterns.

L. B.'s responses included a significant number of exceptional trials in which he was able to name correctly the left as well as the right halves of the chimeric stimulus. This subject shows impressive, presumably re-educative advancements in cross integration in many tests over his condition during the first two years after surgery. Possible interpretations including co-operation of the minor hemisphere in speech, use of mid-brain visual mechanisms, cross cuing or strategies based on differential flux cues remain to be checked and are not critical to the questions concerned here.

Comparisons with a Left-handed and an Ambidextrous Patient

A left-handed commissurotomy patient, P. D., was tested eight months after he underwent surgery at age 27. This patient showed evidence of severe cerebral damage before operation with an IQ below 70. In general he has exhibited a partial mirror reversal of the hemisphere deconnexion syndrome including anomia for right-hand stereognosis and for the right half-field of vision, right hand apraxia for verbal commands, etc., all indications pointing to right hemisphere speech (Bogen and Saul, 1970). Our main objective with this left-hander was to determine whether the minor hemisphere specialization for perceptual functions might also like language have undergone a corresponding shift to the opposite side. In cases of left-handedness associated with brain damage to the left hemisphere perceptual functions are sometimes retained in the right hemisphere along with the additional language load (Zangwill, 1954).

P. D. was given the test involving recognition of familiar objects. His responses with the left hand were quick and the left field stimulus was chosen in every trial. Responses with the right hand were more variable showing some hesitance, double choices, and spontaneous naming although he was instructed not to speak. With the right hand the right half of the chimeric stimulus was selected more than twice as frequently as the left. Both halves were correctly identified in 25 per cent of the right-hand trials. When the test was run with verbal read-out, he shifted back to a correct selection of the left field stimulus on all trials, in direct contrast to the right-field shift shown by the other subjects. The results were thus consistent with the conclusion that the lateral shift of language had not been accompanied by a corresponding switch of the minor hemisphere visual perception functions.

A commissurotomy patient (R. Y.) with an early history of ambidexterity was given all except the chain pattern test at four and a half years after his surgery at age 43. This subject also differed from the others in being older and in having signs of neurological impairment in the bilateral sensory and motor cerebral systems producing an excessive separation in hemispheric function such that use of right or left hand automatically invoked left or right hemispheric control (cf. Trevarthen and Sperry, 1972). This made his scores useless for the main objectives of the present study but brief mention of the results is included here for their interest in other respects.

In manual performance on the face test R. Y. consistently selected the left half of the chimeric figure when he used the left hand and shifted to the right half when he used the right hand. This was true in principle also for the antlers test except that this test was more difficult and he made numerous errors thereby introducing into the score a minority of opposite field choices. In the familiar items test he again chose consistently the left half of the stimulus with the left hand and the right half with the right hand. When the mode of response was changed to verbal naming, his scores on the face test showed a two to one preference in favour of the right half of the stimulus, but R. Y. had great difficulty in learning the names and made many errors. He failed to learn the antler test verbally and his scores remained at chance level. On the test for familiar objects he consistently chose the right half stimulus. In so far as they were indicative of lateral specialization, his scores thus conform with those of the other right-handed subjects.

Discussion

The results show that when right-left pattern chimeras joined at the mid-line are viewed on centre by patients with fore-brain commissurotomy the subjects report no strangeness, discrepancy, or incompleteness in the evoked perceptual image. Even with gross mismatch between right and left halves of the chimeric stimulus, the subjects seemed typically to remain unaware of the discrepancy except when indirect confusion became manifest secondarily as a result of responses by one hemisphere that were recognized to be incorrect by the other hemisphere. In the tests for facial recognition, for example, each hemisphere apparently perceived its own half-face separately and tended to complete the perception by filling in the unseen half of the same face in conformity with earlier studies on perceptual completion (Trevarthen and Kinsbourne, 1972). This general result prevailed with all categories of stimuli that were tested. The presence of a second parallel percept in the non-responding hemisphere may be inferred from those trials in which a routine manual response was blocked without forewarning and the subject then was able on request to provide a correct verbal response that described the image projected to the opposite hemisphere.

The activity of the two hemispheres under these conditions showed consistent left-right differences. The right, minor, hemisphere in these right-handed subjects dominated the response when no language was involved and only a direct manual reaction was required such as pointing to a matching visual stimulus. Since this response involved no more than simple manual pointing with either right or left hand, we may infer that the determining factor in the observed hemispheric superiority lay in the perceptuo-cognitive realm of the cerebral performance governing oculomotor search and retrieval rather than in the executive mechanisms for motor expression in pointing.

Earlier results (Levy-Agresti and Sperry, 1968) raised the question as to whether it is spatial-perceptual transformations which are primarily involved in minor hemisphere specialization or whether the difference rests on a more primitive perceptual capacity like direct apprehension of shape. The present results strongly implicate the latter. Conversely, a distinct deficiency in basic pattern apprehension seems apparent in the present data for the language-dominant hemisphere, supporting the suggestion that the kind of cerebral organization suited for language is poorly structured for perceptual apprehension. In general the results support the view that lateral specialization may be understood as a means of providing for language and related symbolic functions in one hemisphere without handicapping the development of spatial perceptual abilities in the other (Levy, 1969).

It is of special interest that the minor right hemisphere consistently dominated the voluntary motor response in most of the non-verbal tests where the sensory input to right and left hemispheres was essentially similar, even when the major hemisphere was favoured by having the subjects use their right hands. In general the post-operative behaviour of these people has been dominated by the major hemisphere, for it has been difficult to get motor expression from the minor hemisphere except under restricted testing conditions. The present results show, however, that voluntary motor dominance may be exerted directly from the disconnected minor hemisphere under conditions where each hemisphere is allowed free and equal access to the motor system, or even when the left hemisphere is favoured by use of the right hand. With other things equal, restriction of manual responses to a given hand tends to favour control by the contralateral hemisphere. The initial response in the present tests involves an exploratory search with eye and head movements and it is this exploratory search for a visual match that we infer to be governed by the right rather than the left hemisphere.

It is also clear that dominance of the motor expression switched sharply from right to left hemisphere when the instructions required a verbal instead of manual response while the input and perceptual task remained essentially unchanged. The switch to the major hemisphere also brought qualitative changes in the mode of cerebral processing, as reflected in the subject's scores, incidental comments and introspections. With the major hemisphere in command the recognition process tended to be more analytical. The major hemisphere kept searching for distinctive subordinate features that could be handled verbally. It seemed unable, for example, to recognize or remember a face as a whole, needing instead to pick out some analytical detail to which a verbal label could be attached. All four of the present tests confirmed in different ways the presence of a fundamental difference in the way the right and left hemispheres perceive things. More than a slight preference in a competitive situation, the results suggest a strong basic differentiation. Where the kind of task being tested could be performed by either left or right hemisphere, the two hemispheres accomplished the same task by characteristically different strategies.

It appears from the results that the left hemisphere became dominant when some form of verbal and/or conceptual, symbolic transformation was required. When immediate recognition and memory of visual shape was the only requirement, even though a stimulus possessed a well-known name, the right hemisphere dominated. This finding appears to be relevant to the problem of visual-verbal encoding in the normal brain, and suggests that verbal encoding, in contrast to proposals by many authors who are impressed by the role of verbalization in short-term memory retention (Conrad, 1962; Glanzer and Clark, 1962, 1964; Lantz and Stefflre, 1964; Wickelgren, 1965; Neisser, 1967; Brewer, 1969; Colegate and Eriksen, 1970), does not occur automatically for visual stimuli in general. In fact Bahrick and Boucher (1968), Taylor (1969), and Cohen and Granström (1970) have shown that visual material may be stored in a visual code without recourse to verbal labelling. It appears that not only are different encoding strategies normally present but that, as in the commissurotomy patients, one strategy, the non-verbal, is more basic for visual recognition and predominates unless there is a specific requirement calling for the other.

The exceptional double responses in which L. B., A. A. and C. C., but not N. G. or R. Y., correctly described or named both left and right halves of the composite stimuli occurred well above a chance level. Vocal description of left field stimuli stands in contradiction to the typical response capacity of these subjects and accordingly requires explanation. Presumably it reflects the effects of post-operative training and re-education. Whether the minor hemisphere was co-operating in the verbal report, or whether both halves of the visual field were reaching the verbal hemisphere, or whether a unified mid-brain perceptual awareness was involved, or some combination of these, cannot at present be determined from the data available. The extreme to which such left-right cross integration can be achieved in the absence of the corpus callosum is illustrated in "asymptomatic" patients with total agenesis of the corpus callosum (Sperry, 1970). Regardless of their future explanation, these double responses provided little information which was of use in assessing left-right differentiation in mental capacities.

While the results of the face and antler tests show a minor hemisphere superiority in both cases, the present data in no way exclude the possibility that face recognition is a special ability beyond that for general form apprehension. The two tests involving items with well-known names showed the same minor hemisphere dominance with pointing read-out as did the tests involving items having no verbal labels. In view of evidence (Milner, 1967) indicating a right hemisphere perceptual superiority specific for shapes having no verbal labels, these results were somewhat unexpected. A possible explanation of the discrepancy may be found in the degree to which a verbal encoding bias is involved in the test design. No verbalization was required in the present tests. Our results conform with the assumption that visual retention for direct matching encoding is done by the right hemisphere, and verbal encoding by the left and indicate further that in the absence of biasing influences, the primary tendency is for all visual stimuli to be perceived in the minor hemisphere.

Summary

Visual testing with composite right-left chimeric stimuli shows that the two disconnected hemispheres of commissurotomy patients can process conflicting information simultaneously and independently. Which hemisphere dominates control of the read-out response was found to be determined primarily by the central processing requirement rather than by the nature of the stimuli or whether the response is ipsilaterally or contralaterally mediated. Where the task needs no more than visual recognition, a visual encoding ensues, mediated by the right hemisphere and based on the form properties of the stimulus as such rather than on separate feature analysis. On the other hand, where some form of verbal encoding is specifically

required, the left hemisphere takes over and attempts a visual recognition based on nameable analytical features of the stimulus. Stimuli having no verbal labels stored in long-term memory and which are resistant to feature analysis were found to be extremely difficult for the left hemisphere to identify. We conclude that each of the disconnected hemispheres has its own specialized strategy of information processing, and that whether a hemisphere is dominant for a given task under the test conditions depends upon which strategy is the more proficient.

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(*Received 17 June 1971*)

Printed in England
by
STAPLES PRINTERS LIMITED
at their Stratford, London establishment