PLATE XLIV

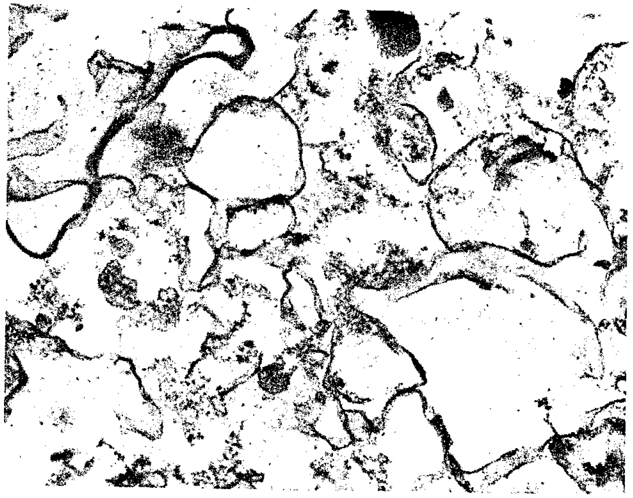

FIG. 3.

FIG. 4.

FIG. 5.

To illustrate article by H. Savolainen and J. Palo.

Brain (1973) **96**, 547–570

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PERCEPTUAL UNITY OF THE AMBIENT VISUAL FIELD IN HUMAN COMMISSUROTOMY PATIENTS[1]

BY

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INTRODUCTION

STUDIES on a group of 10 commissurotomy patients of Vogel and Bogen (Bogen and Vogel, 1962; Bogen, Fisher and Vogel, 1965) show that stimuli presented tachistoscopically in the right and left halves of the visual field are perceived separately in the disconnected hemispheres (Gazzaniga, Bogen and Sperry, 1965; Sperry, Gazzaniga and Bogen, 1969). The perceptual experience of each hemisphere appears to remain outside the conscious awareness of the other, and little or no overlap is found at the vertical mid-line (Sperry, 1968, 1970). The loss of interhemispheric communication is evident in the inability of the split-brain subject to interrelate stimuli seen in left and right visual fields or to verbally name or describe objects and patterns presented in the left half-field of vision. When visual material is presented in the left half-field, the subjects have appeared unable to report anything but the onset or offset of light, or very gross brightness or directional differences, and they deny having seen any discrete item.

Considerable evidence has been advanced recently for the existence of a hierarchical organization of visual mechanisms in primates (Trevarthen, 1968): two main systems are distinguished, one cortical for focal and identifying functions centred on the fovea, and another more mid-brain dependent that subserves orientation in ambient space and is correspondingly more sensitive to peripheral vision and to motion effects by which space is apprehended. Some of the initial evidence has come from bilateral integration of visual function in split-brain monkeys, and it therefore seemed a plausible possibility that neocommissurotomy in man may also divide cortical vision for perception of detail and identification of objects, without producing a similar division in the perception of ambient space.

Most of the earlier studies of vision in these patients have used stationary stimuli presented at 1/10 sec or less. This testing procedure may have selectively favoured

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cortical vision and predisposed against ambient or mid-brain vision, leaving undetected any latent cross-integration between left and right visual fields based on mid-brain mechanisms. We describe an attempt to search further for cross-integration between the half-fields of vision in these same patients with methods selectively designed to favour ambient rather than focal vision.

Apparatus and Methods

Large projection screens were used for peripheral stimulation on both sides of the subject. A semicircle of thin, white, translucent plastic, radius 15 in., filled the visual field of the subject to 90 degrees from the central fixation point on each side and to 45 degrees above and below the horizon (fig. 1A). This screen was used for initial tests with slide projectors. Later it was replaced by a pair of 24 in. × 24 in. flat "Polacoat" screens (glass with a matt plastic film applied to one side) mounted at right-angles (fig. 1B).

Stimuli were projected with two 100 watt, 35 mm slide projectors, or two concentrated-arc lamps (point sources). The latter were 25 watt Argon-filled arc lamps with light sources 0·8 mm in diameter. Back-projection was employed, the light sources and stimuli being manipulated by the experimenter on the opposite side of the screen from the subject. The biplanar screen was used for all tests with the point sources. The perimeters of both cylindrical and biplanar screens were marked out in visual degrees for recording of stimulus locations. In addition, the area between each point source and the screen was ruled to permit plotting of the depth location of the virtual image perceived by the subject on the other side of the screen (fig. 1B).

The screens were on a low table and the subject's seat height was set to bring the fixation point to eye level. In most tests the middle of the field was blocked out to produce a central gap of 20 degrees to 60 degrees in which no stimuli appeared.

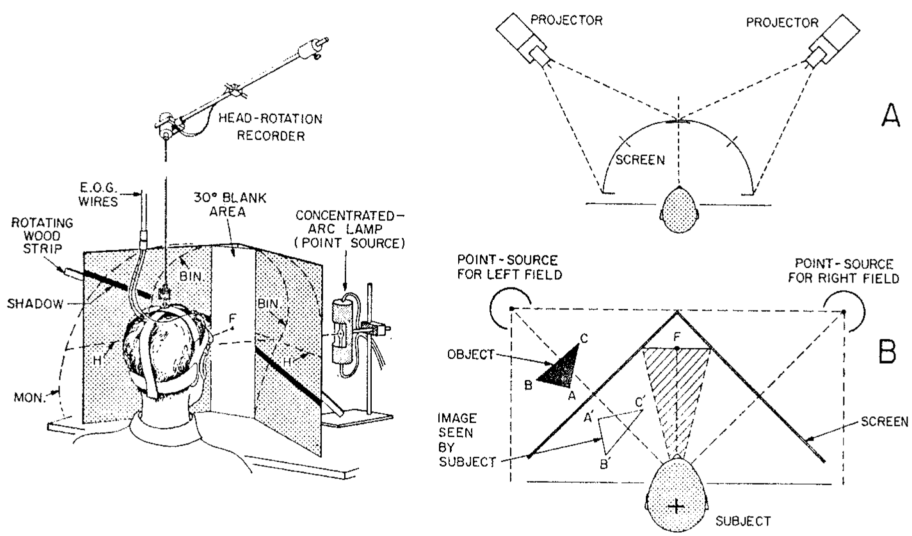

FIG. 1.—*Left:* Recording head and eye rotations while subject cross-matches shadows. Limits of monocular (MON) and binocular (BIN) visual field. *Right:* Plan views of test screens. A, Semicircular screen and projectors. B, Biplanar screen with point-source lamps.

Shadows and silhouettes were moved in the panoramic field provided by the screens. Patterned stimuli were produced with photographic slides or, in the case of tests with the point source lamps, with perforated metal sheets, black tape applied to thin glass sheets, metal mesh, or opaque objects supported on thin rods or threads. These objects were coated with black matt paint to eliminate reflections (fig. 7).

Tests of motion perception were made by moving objects between the point source and the screen to make shadows of various sizes and varying rates of motion at different locations in the field. Stimuli were displaced by hand at carefully regulated known rates, or they were rotated or moved up and down in sinusoidal motion with small DC motors.

Point source, or polar shadow-projection enables one to produce parallactic transformations of shadows giving the appearance of displacement and rotation of rigid or non-rigid 3-D objects variously located in the space around the subject. The shadows cast by objects placed anywhere between the source and the screen are always sharp. The principles of this form of projection and its advantages for studies of visual perception have been described by Gibson (1957) and by Gibson and Gibson (1957).

Coloured stimuli in motion were produced by moving Wratten filters in the projectors. The colours employed are given in the Results. Discrimination of complementary colour patches in the left field was tested by projecting the two complements with two projectors on to the left screen, the intensities of the light being adjusted so that a mixture close to white was produced where the light from the two projectors overlapped. Shadows cast in front of one projector at a time were then visible as brightly illuminated in the colour produced from the other projector. Thus, if red and green lights were projected overlapping to make white, a shadow cast in the red projector appeared bright green on a white background.

Before testing, the subjects were adapted to a reduced level of artificial light (approximately 5 Ft. Cd.). The white light of the stimulus screens was kept at between 20 and 50 Ft. L. Against this, silhouettes of black velvet had a luminance of 0·2 Ft. L., and projected shadows varied between 1 and 3 Ft. L.

The levels of illumination were adjusted so that no scattered light or unintended reflections were visible to provide uncontrolled cues. Drapes of black velvet were employed to cover parts of the field outside the area of stimuli, for example when stimuli were restricted to the left half of the field, and to further reduce or remove reflected light. Additional precautions used with colour stimuli are described below. The effectiveness of the foregoing controls was confirmed in blank tests. In discrimination tests the different stimuli were presented in an unpredictable order based on a balanced pseudo-random sequence. The examiner was not visible to the subject while he was presenting stimuli and recording responses.

All verbal responses of the subject were recorded for subsequent evaluation and in addition the microphone signal was carried to the polygraph so that response latencies could be determined. Sound-television recording on audio-visual tape was employed in all critical experiments to check on movements of the body and limbs of the subject during testing, and to correlate responses with stimulus transformations. The television camera was mounted from the ceiling and outside the visual field of the subject. Hand movements, subvocal speech movements, involuntary eye movements and other behaviour correlated with stimulus presentation were watched to check on possible cross-communication between the two halves of the brain through peripheral channels. All slow or protracted responses were noted.

Throughout all tests, horizontal displacements of the eyes and horizontal rotations of the head were recorded by the method of Trevarthen and Tursky (1969). A cloth harness was fitted on the subject's head for attachment of a counterweighted apparatus with which head rotations were measured. Eye movements were detected by miniature electro-oculographic electrodes, and the eye rotation signals were calibrated to equal the head rotations by asking the subject to maintain fixation on a point while turning his head from side to side in an arc of approximately 60 degrees. The two unfiltered DC signals of eye rotation and head rotation thus equated were summed to obtain a continuous tracing of the horizontal direction of regard on a Beckman polygraph, along with a stimulation artifact. By this means it was possible to verify visual fixation to within 2 degrees of arc throughout the tests, and to obtain a permanent record of any displacement of gaze which the subject made in spite of instructions to fixate.

Trials in which eye movements occurred, possibly displacing visual stimuli over the vertical meridian, were discarded, and a tally was made of involuntary eye movements made at the time of response or between presentations of visual stimuli. Representative eye-movement tracings are shown in fig. 2.

Two main kinds of experiment were performed, one involving cross-integration of visual stimuli on both sides of the vertical meridian, the other requiring the subject to make verbal responses to stimuli confined to the left half of the visual field.

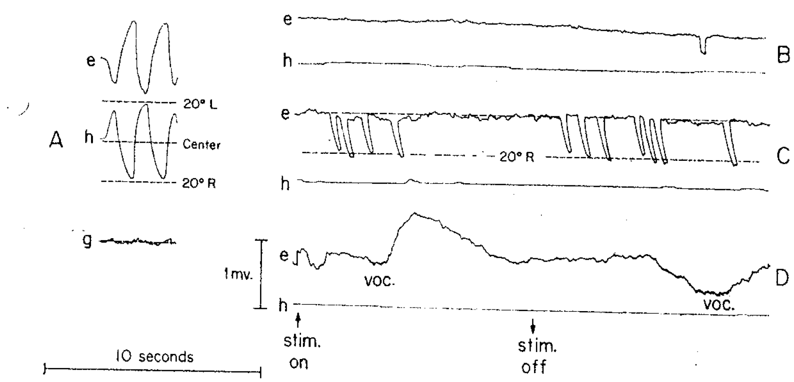

FIG. 2.—Eye movements. A, Calibration of EOG against head rotation. B, Steady fixation. Some drift of EOG. One glance to right. C, Involuntary glances to the right. D, Changes in skin potential (GSPs) and myogram of speech movements. Stimulus: red light appearing in left field. e=EOG; h=head rotations; g=gaze (=e plus h); voc=vocalization.

MATERIAL

Subjects.—We are indebted to Drs. P. J. Vogel and J. E. Bogen for clinical information. The commissurotomy operations were performed by Dr. Vogel and his staff at the White Memorial Medical Center in Los Angeles.

L. B. (Bogen, 1969): A schoolboy, 17 years of age at the time of testing had a history of convulsions since age 3, presumably the consequence of brain injury at birth. He was operated upon when 13 on April 1, 1965. All interhemispheric commissures were sectioned. His post-operative recovery was remarkably rapid and uneventful, and since operation he has only had rare minor seizures in which the left side of his body was most affected. He is alert and talkative with a preference for solving problems verbally. His post-operative scores on the WAIS intelligence test administered in May 1968 were IQ, 106; verbal, 110; performance, 100. At school, however, though he performs moderately well at times, he appears to suffer from inability to sustain attention, and inadequate memory. He shows right-eye dominance, and a tendency to loose convergence by deviation of the left eye with which he reports monocular diplopia. He wears glasses to read.

A. A. (Bogen, 1969; Nebes, 1971): A 19-year-old boy at time of these tests attends a school for the handicapped. He was delivered by forceps following an induction because of toxæmia, and he had convulsions with fever at age 4 months. Generalized convulsions, sometimes beginning in the right arm, recurred at age 5 and thereafter. He was slow in speech and somewhat ambidextrous before operation. This was on October 14, 1964, at age 14 and was difficult. The corpus callosum

and anterior commissure, and presumably the hippocampal commissure, were sectioned. The massa intermedia was not seen. In consequence of right cerebral swelling he exhibits a spastic left leg and a positive Babinski sign. His left arm recovered well. Since the operation his right hand shows relative insensitivity and he experiences occasional numbness of the right arm with incoordination and often with arrest of speech. He speaks slowly and shows considerable intellectual impairment. His WAIS intelligence score in August 1968 was: IQ, 78; verbal, 77; performance, 82. He shows a slight attentional bias favouring the left eye.

N. G. (Bogen, Fisher and Vogel, 1965; Bogen, 1969): A 37-year-old housewife and mother who had her first convulsion at age 18 when she was four months pregnant. Her family has a history of epilepsy. When she was admitted to hospital for examination in 1952 an EEG showed left temporal slowing and X-ray revealed a calcification 1 cm in diameter beneath the right central cortex. She continued to have vacant episodes ("strange feelings" in the left side of her body preceding her convulsions) and generalized convulsions which progressed into status epilepticus.

She was operated upon on September 5, 1963. Corpus callosum, hippocampal commissure, anterior commissure, massa intermedia, and right fornix were sectioned. A vein draining the right parietal area was divided. Her immediate post-operative recovery was satisfactory, though in the first week she exhibited inactivity of the left side, disturbance of speech and failed to recognize her husband. Disorientation for time and poor recall for recent events persisted for several weeks. Generalized convulsions experienced shortly after operation have been controlled by medication which is now reduced, and her condition seven years later is excellent. She has good use of both hands. She is right eye dominant. When left to guide herself in less familiar surroundings she becomes easily lost and has a tendency to turn to the right when faced with a choice of direction. Her WAIS score, in August 1968, was: IQ, 77; verbal, 83; performance, 71.

R. Y. (Bogen, 1969): A 47-year-old man at the time of these tests is jobless and cared for by his relatives. He was hit by a car at age 13 which resulted in a closed head injury. At age 17 he first had generalized convulsions. Cerebral commissurotomy was performed on March 7, 1966, when he was 43. The corpus callosum and anterior commissures were visualized and completely divided. He recovered from operation satisfactorily, was speaking well and obeying instructions the day after, but he showed unresponsiveness of the left arm and hand which persists to a slight degree. He speaks well and enjoys conversation, exhibiting a tendency to repetition of his stories and he becomes silent and disorientated when taxed. He occasionally is discoordinated in actions with his left hand and reports that quite often his two hands act in conflicting ways. In testing situations his left hand becomes subject to periodic involuntary behaviour in response to extraneous stimuli. His WAIS score in August 1968 was: IQ, 90; verbal, 99; performance, 79.

L. B. was more intensively tested than the others because conditions in this subject most favoured the cross-integrative phenomena of the present study. He had least evidence of brain damage before operation, was youngest at the time of operation and made the most smooth and rapid post-operative recovery. Following exploratory tests, the phenomena were accordingly pursued in more detail in L. B. with some later follow-up in the other subjects to obtain comparative data.

RESULTS

I. Right-Left Cross-Integrations

(*a*) *Verbal response to simultaneous stimuli either side of the meridian.*—After he had learned to control effects of reciprocal extinction of one stimulus or the other and to maintain his gaze steady on centre, L. B. reported that he could see simultaneously two 10 degree circles of white light located one each side of the fixation point at 45 degrees from the centre. When the circles were moved together through 10 degrees to 20 degrees in one second, he was able to say whether both went "up," or "down," or whether the pair "twisted," one moving up while the other went down (fig. 3, test A). In 16 trials, comprising 4 of each coupled pattern of motion, he made 2 errors. In both of these he appeared to neglect the left stimulus, basing his response only on the motion in the right field. The probability of obtaining this score while attending to one side at a time is less than 0·01. His gaze remained absolutely fixed at the centre of the field throughout this run, and he made no hand movements.

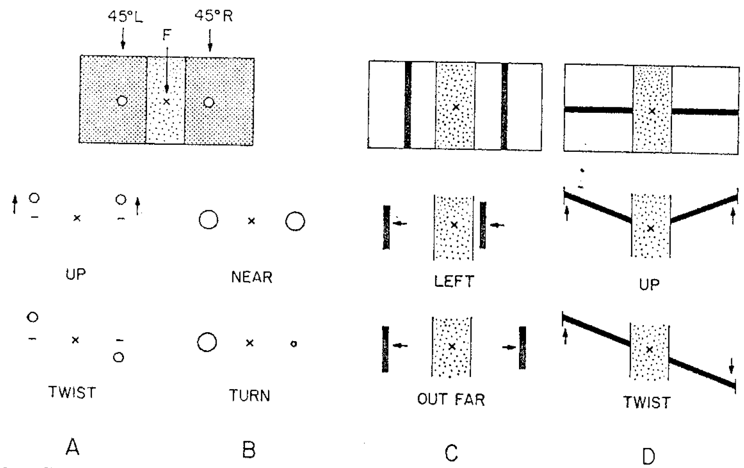

FIG. 3.—Cross-matching with simultaneous stimuli. A, 10 degrees circles displaced vertically. B, Circles changing in diameter. C, 5 degrees vertical shadows displaced sideways. D, 5 degrees shadows pivoted at fixation point. × = fixation point.

At the conclusion of this test, L. B. spontaneously reported the motion of the lights in two additional trials in which they were displaced, without warning, toward each other and then further apart. He said "in close" and "out far," each with a latency of less than 1·5 seconds after the start of the movement.

The circles of light were then expanded to 15 degrees, or shrunk to 5 degrees, by displacing the perforated sheet toward or away from the point source. L. B. reported whether the stimuli appeared to move "near" or "far," or in a coupled unlike motion which he called "twisting" (fig. 3, test B). He was as accurate as in the previous run and he kept steady central fixation. In repeat runs, L. B. reported the relative positions and sizes of the two stimuli in the above tests when they were motionless at the end of a displacement. He accurately reported which of the two was bigger, or closer to the mid-line, in a significant proportion of trials.

Comparable verbal reports were obtained with pairs of 5 degrees, black, vertical shadows, one on each side, which were moved simultaneously further apart, nearer together, or both to the right or both to the left (fig. 3, test C). All displacements were made between 30 degrees and 70 degrees from the fixation point. In 32 trials L. B. made one error ($P < 0{\cdot}01$, with attention to one side only). Once again, this error appeared to be a consequence of temporary neglect of the left. His eyes remained steadily fixated on centre throughout this test also.

L. B. correctly cross-integrated the coupled displacement of 5 degrees black shadows pivoted at the centre of fixation, behind the 40 degrees central blank area (fig. 3, test D). On each trial, the stimuli were first brought horizontal, then they were removed together (20 degrees to 30 degrees in 0·5 to 1·0 second) to both up, or both down positions, or to a left-up or right-up tilted position with the two diagonals in line. In 32 trials he made 2 errors ($P < 0{\cdot}01$, with attention to one side). He maintained steady fixation on all trials.

Subjects A. A. and N. G. were also able to perform these cross-integrations between paired stimuli on right and left. R. Y., however, either failed to respond verbally to the visual displays or completely neglected the left stimulus, reporting the direction of motion on the right only. The results with L. B., A. A. and N. G. on all cross-integration tests are shown in Table I.

TABLE I.—SCORES IN CROSS-INTEGRATION TESTS

	Motion of stimuli					
	Like		*Unlike*		*Errors due to*	
	Correct	*Errors*	*Correct*	*Errors*	*Left neglect*	*Right neglect*
L. B.	39	1	36	4	4	0
A. A.	41	7	34	14	12	2
N. G.	54	10	31	33	33	0

Table I shows that both left and right stimuli were perceived together in most of the trials ($P < 0{\cdot}01$ for each subject), but all three subjects scored significantly better for those trials in which the motion of the stimuli was the same on both sides of the vertical meridian. This was apparently due to periodic neglect of the left stimulus. For these trials a response to either side alone would be correct.

A. A. scored nearly as well as L. B., but N. G. responded to the right stimulus alone in about half of the trials in which the two stimuli had unlike motion. None the less, taking account of this, N. G. did discriminate like from unlike coupled motions in approximately 50 per cent of the trials ($P < 0{\cdot}01$). Each of the subjects was consistent in his or her performance, scores for the different cross-integration tasks being closely similar in each case.

The effects of perceptual neglect or one-sided visual attention were clear in the responses of all subjects in a variety of tests performed in preparation for the above. When they kept central fixation, all subjects initially failed to report both stimuli when circles of light or black shadows were introduced into left and right fields. Indeed, their performance with single peripheral stimuli appearing from the lateral edge of one field and moving slowly toward the centre strongly suggests that, compared to normal subjects, the commissurotomy patients have grossly impaired attention, or contracted visual fields.

The results in Table I show that neglect of the left side was strong in the case of N. G., less strong in A. A. and least in L. B. R.Y. could say when motion occurred in either left or right fields alone, but he always reported the left stimulus as weaker, and double stimulation produced almost 100 per cent extinction of the left side when he was making vocal responses.

All subjects showed occasional arrest or confusion of speech when they were attempting to respond to the two sides. L. B., A. A. and N. G. lost speech more frequently when they were attempting to describe coupled unlike motions, i.e. they mumbled or struggled to recall words like "twisting" or "turning" even though a few seconds earlier these same words had been produced in correct responses. Their behaviour suggested immediate perception of the coupled motions, but loss of vocal response. N. G. blushed and large galvanic skin potentials were recorded in the EOG leads immediately after visual stimuli for which she could give no accurate verbal response. Bilateral visual stimulation commonly caused R. Y. to become totally mute. He remained arrested on the fixation point and attentive. When questioned, he was confused and said that he had been watching both stimuli move.

The results are corrected for involuntary displacements of gaze, all trials showing a shift of fixation at the time of stimulation, or between the stimulus and a response, being culled out. An asymmetry was apparent in the involuntary reorientations made in spite of instructions to fixate the centre. All four subjects made glances to the right lasting 0·2 to 0·5 second (fig. 2). Most of these eye movements were to the right edge of the central blank area (20 degrees to the right), or to some point central to this (i.e. 10 degrees to 15 degrees to the right).

Barrages of right glances were significantly correlated with *lower* scores, when the subject was distracted or confabulating. The most correct runs of trials occurred when the subject was keeping steady fixation and was responding in a quiet, automatic manner. Involuntary eye movements followed errors, distracting noises or conversation.

There were consistent differences between the subjects. L. B. and A. A. kept steady fixation for minutes at a time while cross-matching the peripheral stimuli. N. G. appeared to have hyperactive oculomotor reflexes and had considerable difficulty keeping her eyes on centre. R. Y. kept his gaze steady for attention to moving peripheral stimuli, especially when mute, but he could not control his fixation when he attempted to give verbal reports.

The cross-integration test in fig. 3D was repeated with the subject instructed not to speak, but instead to follow the stimuli with corresponding movements of right and left hands positioned horizontally with fingertips touching in the mid-line just below eye level, between his face and the screen (fig. 4).

The results, recorded on videotape and subsequently analysed, were closely comparable to those obtained with verbal report.

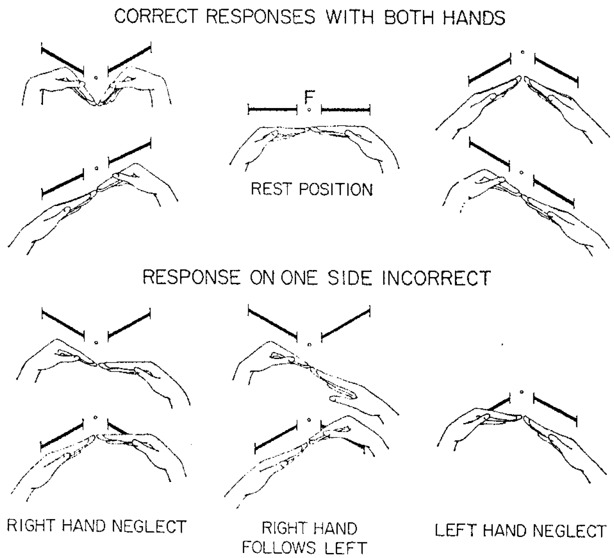

FIG. 4.—Hand movements in response to diagonals as in fig. 3D.

R. Y. made mirror symmetric movements for all stimuli, or neglected the left side. The other three subjects each initiated correct responses in a significant number of trials, with gaze centred. They all showed signs of motor conflict. L. B. tended to neglect the right stimulus, N. G. failed more frequently with the left. The latencies of first hand movements were the same as for verbal responses, or longer (1·0 to 2·0 seconds), making it therefore unlikely that invisible body adjustments could have provided proprioceptive cross-cueing for the verbal responses.

(*b*) *Locating the midpoint of a line joining two right and left stimuli at different levels.*—This test was devised to obtain a measure of the accuracy of perception of

the relative height of two stimuli appearing simultaneously to left and right of the centre of the field. Dark 2 degrees-wide shadows were made to project 5 degrees from the edge of a central blank space 40 degrees wide for approximately one second. The shadows appeared in pairs at one of 5 positions on each side, as shown in fig. 5. In a run of 24 trials in an unpredictable order, each of the 8 pairs connected by diagonal broken lines in fig. 5 appeared twice, and the horizontal pairs BB and DD appeared four times each. The subject was instructed to give the location on the mid-line where he would judge the centre of a line connecting the two stimuli to fall. Correct responses were demonstrated in preliminary trials. In each trial the location of the point chosen by the subject was noted on a 9-point scale (points 1–9 in fig. 5). For spoken responses, the subject said "top" (above point 4), "middle" (between 4 and 6), or "bottom" (below point 6) to indicate where he perceived the midpoint of the imaginary line joining each pair of stimuli.

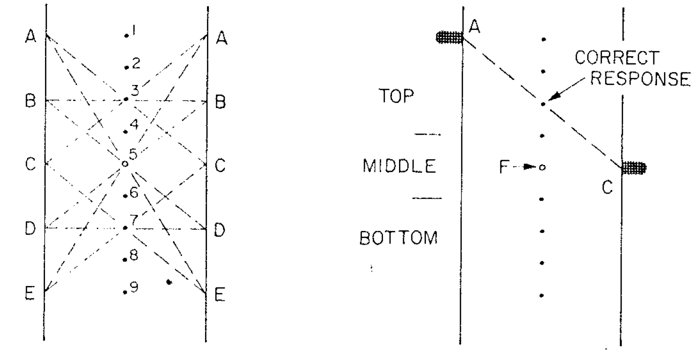

FIG. 5.—Choosing the midpoint.

The results for this test are summarized in Table II. L. B.'s responses approximated the correct mid-point. He reported that the task was not difficult and that he could see both stimuli at once. His responses were cautious but not unduly slow, nor were they misdirected with respect to the mid-line fixated. Once he responded only to the right stimulus with the right hand, and once only to the left stimulus with the left hand. There is no evidence of neglect of the left side with verbal responses. His eyes remained fixated while the stimuli were presented and until the response was completed.

A. A. showed a strong tendency to respond only to the left stimulus, even when pointing with the right hand or reporting verbally where the mid-point appeared to be. Nevertheless, he said he saw both stimuli well. His eyes were very steady for each run. The movements of his right hand were exceedingly slow. Twice he aimed his hand first toward the right side of the centre area, then slowly brought it to the mid-line. His verbal responses were weak and slow with a latency of one to three seconds. In three trials he appeared to have responded only to the right stimulus.

N. G. responded well with her right hand, attending to both stimuli, but at the same time reaching about one point too high. This was true even for the horizontally aligned pairs BB and DD. Allowing for this, her score shows evidence of partial unilateral neglect favouring the right stimulus but it proves she could integrate the stimuli on both sides to govern her response. In 5 trials she aimed her index finger approximately one inch to the right of the mid-line. She kept steady fixation in this run. With the left hand, however, she showed a strong attention bias favouring the left stimulus and, in addition, she repeatedly misaimed her response far to the left of the mid-line. With the left hand she also became more confused, making many eye movements and twice shaking her head with an involuntary vocalization after making her response. When responding verbally she acted as if she were seeing only the right stimulus.

TABLE II.—RESULTS OF "CHOOSE-THE-MIDPOINT" TEST

		Left only	*Half left*	*Centre*	*Half right*	*Right only*
L. B.	R. hand	0	5	7	3	1
	L. hand	1	3	8	4	0
	Voice	2	—	8	—	3*
A. A.	R. hand	11	2	3	0	0
	L. hand	8	7	1	0	0
	Voice	9	—	0	—	3*
N. G.	R. hand	1	2	7	4	2
	L. hand	5	9	2	0	0
	Voice	0	—	2	—	10*

* With spoken responses, ambiguous choices, which might have been either correct or the consequence of neglect of one side, are excluded. There were 16 trials in each test. Left (right) only=Response within one point of opposite the left (right) stimulus. Half-left (right)= Response between correct (on centre) and level of the left (right) stimulus. Centre=Response at correct mid-point in the line between left and right stimuli.

(*c*) *Cross-matching a stimulus in one field to one previously set in the other field.*— Measurements were made of the accuracy with which the commissurotomy subjects could set a 2 degree black bar pivoted at the fixation point in line with a similar diagonal on the other side.

The stimuli were shadows cast by point-source lamps of thin balsa laths which were turned silently 2 cm behind the screens. The experimenter first set the cue stimulus at 15 degrees up or down, then the stimulus on the other side was rotated at approximately 10 degrees/sec until the subject signalled "stop" when he judged the two halves of the display to be in line (fig. 6, left). In each run of 16 trials, motion of the second line began either in the same direction as the present cue line or in the opposite direction with equal frequency for each cue stimulus position. The latter was up or down eight times in each run, alternating on an unpredictable schedule. After each trial both stimuli were brought to horizontal. If the subject did not respond at the correct place, the motion of the second stimulus was reversed when it had reached 45 degrees up or down: i.e. one cycle of positions was completed. Six runs were made, two for each of three modes of response: tapping the table with left hand, tapping with right hand, or saying "stop" to indicate when "in line" setting had been reached. For each mode, there were 16 settings with the cue on the left, and 16 with the cue on the right for a total of 96 trials.

The responses of L. B. are shown in fig. 6, left. Half fell within ±5 degrees of the correct position. Incorrect mirror settings occurred twice for the left cue with the left hand, once to a right cue with the right hand, and three times to a right cue with verbal response. The subject kept steady fixation in all trials, but made involuntary visual orientations (which usually involved head rotation) to inspect his result 0·5 to 2 seconds after responding in 32 of the 96 trials. There was a bias in favour of inspection of the right half of the display (22 of 32 orientations) which was stronger for the left hand (13 of 15) than for the right (6 of 12). This indicates that the subject was primarily looking at the field for which the hemisphere most probably active (because contralateral to the hand responding) had poor visual reception. The total bias to look right, in spite of the fact that two-thirds of the responses were of a kind expected to favour the left hemisphere, may, therefore, be a consequence of an intrinsic lateralization in visual attention favouring the *right* cerebral hemisphere.

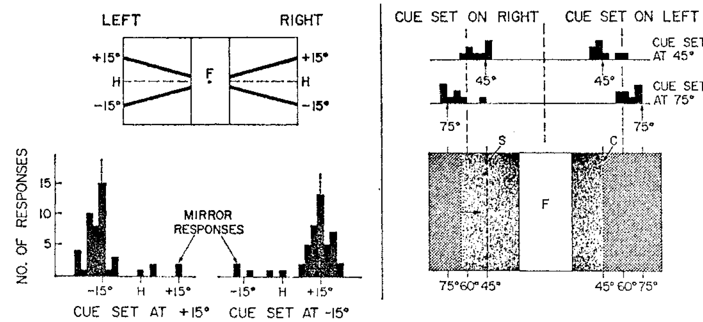

FIG. 6.—*Left:* Lining up diagonals across the field. *Right:* Setting vertical boundaries between coarse and fine checks to equidistant from centre.

In this test N. G. made 50 per cent of her settings within 5 degrees of correct, but her responses were considerably less precise than those of L. B. In early practice tests she made several mirror settings. In the formal test, when matching the left line to settings of a cue line on the right, 80 per cent of her responses fell 5 degrees to 10 degrees outside the correct position; too high for the +15 degrees target, too low for the −15 degrees position. In contrast, with the cue on the right, 50 per cent of her settings on the left averaged approximately 5 degrees too close toward the horizon. These markedly reciprocal results suggest a perceptual asymmetry with contraction of the left field or magnification of the right. There were no clear differences between the settings with the three different modes of response: voice, right hand, or left hand.

N. G. was unable to suppress a profusion of 0·5 second glances away from the fixation point. The total time for all trials between setting of the cue stimulus by the experimenter and the subject's response was measured. For about half this time her gaze was directed to the right or to the left of the fixation point. Of this half N. G. spent approximately 90 per cent looking right, but less than 10 per cent looking left. Eye movements were mostly to points within the central blank area, with approximately 20 per cent of the glances reaching the edge. Rightward eye movements were significantly more numerous with vocal and right hand modes of response and also when the experimenter set the left diagonal and the subject responded by stopping the right stimulus—all conditions that would seem to favour attention by the left cerebral hemisphere toward the right half of the field.

R. Y. was unable to complete a full set of trials. He failed to see both stimuli or became unresponsive. Attention to the full set of conditions required for successful performance of cross-matching without displacement of gaze proved difficult and tiring for him. In exploratory runs he made several mirror settings and exhibited surprise at the result when he was allowed to shift gaze to inspect what he had done. When responding verbally to set a right stimulus in line with one on the left, he could make settings within ±10 degrees in about 50 per cent of trials and again made several mirror settings. When, however, the right stimulus was the cue, R. Y. was unable to say when the left should be stopped to produce a straight line. He became mute with his attention fixed to the moving stimuli. With the right hand he showed a strong tendency to blindness for the left field and made many eye movements, most to the right. With the left hand he made inaccurate settings and again displaced his gaze in glances to the right, especially when attempting to set the right stimulus to a cue on the left. He made rapidly repeating, apraxic movements of his left hand when attempting to signal with it.

This test was not given to subject A. A.

In a second experiment of this type, L. B. cross-matched the vertical boundaries between check patterns of differing fineness (black squares of 1 degree or of 0·5 degree), but with the same overall black/white ratio (fig. 6, right). One boundary was first displaced, in 2 to 4 seconds, from a point at 60 degrees from the centre of the display to either 75 degrees or 45 degrees on the left or right. The subject was then required to signal when he saw the two boundaries equidistant from the centre. The second boundary was displaced from the 60 degrees mark in one direction and, if necessary, back again. The subject was to keep his eyes fixated on a white spot in the middle of a central dark area 40 degrees across. Lateral displacement of the checkered patterns caused small involuntary nystagmic tracking movements of the eyes in many trials. These were, however, considerably less than 20 degrees and did not shift fixation outside the central zone.

Settings achieved by L. B. show that he perceived the approximate balance of the stimuli, but that he had a tendency to set too close toward the 60 degrees resting position of the display. He had seen both the stimuli in this position with free visual inspection, and presumably he could remember this configuration, with either hemisphere.

In this and in the preceding test, the time interval between setting of the first stimulus and the response varied erratically between 5 and 20 seconds. No clue to the correct time of response could be obtained by counting. There were no visible movements by the subject capable of cross-communicating via peripheral receptors or feedback, and no informative response was detected in the recordings from head and eyes or in the voice recordings. All evidence indicated that the settings were achieved on visual-spatial information obtained from both sides of the field.

II. Verbal Responses to Left Field Stimuli

(*a*) *Detection of visual change. Approximate limits of sensitivity.*—When concentrating on detection of a simple change in the left field, L. B. responded with normal latency and accuracy to a wide range of stimuli. For example, he reported accurately and promptly by saying "now" when a 2 degrees spot of white light moving at 5 degrees/sec entered either at the 90 degrees left edge, or along the top or bottom of the left field. He reported equally well a 0·5 degree-wide, dark shadow penetrating 1 degree to 2 degrees into the field within half a second. Appearances and disappearances ("on" and "off" changes), as well as displacements of dark or light spots 0·5 degree in size anywhere in the field, were immediately signalled by words like "now," "yes," "no," according to questions asked, provided he was attending to the left side. Faint and blurry shadows moved in the field, changes of brightness of spots of light, changes of colour and colour-shadows in patches of light, and translational or rotary motions of the shadows of objects suspended in front of the point source lamps were all responded to quickly. All of the foregoing responses were highly subject to interference and failure if L. B. was at all distracted, or if he had been occupied in conversation (left hemisphere activity) before the stimuli were given. Perceptual neglect led sometimes to complete inability to see even large contrasting stimuli, such as displacement of a 20 degrees patch of light at 45 degrees left. Neglect of a left field stimulus with verbal report that nothing could be seen was frequently observed at the start of a testing session before L. B. had developed sufficient concentration of his attention on the task.

In general L. B.'s best sensitivity threshold in the tests with moving stimuli on the left compared with that of a normal subject. He detected motions of an 0·2 degree dark speck at 45 degrees left, but displacements of 0·5 degree in one second were not detected. He reported the motion of groups of shadows of dust particles on glass held in front of the point source lamps when these shadows were as small as 0·1 degree. Changes in dimensions of the projected shadows of rotating stimuli which he described as moving were of the order of 0·2 degree to 0·5 degree in one second.

The best performance of the remaining subjects with simple left-field motion stimuli was like that of L. B., though N. G. and R. Y. were less responsive and more prone to extinction of perceptions in the left field when they were attempting to speak. Both these subjects were unable to report far peripheral stimuli in either left or right field at the start of the testing session. Such peripheral neglect was most marked with N. G. who frequently appeared less responsive to right stimuli than she was to left stimuli. A. A. responded equally well on left and right sides to these stimuli.

(*b*) *Discrimination of alternative directions of visual change.*—Kinds or directions of change of stimuli located between 30 degrees and 60 degrees left of fixation were accurately described by all subjects. Patches of light or dark of 5 degrees in size were correctly said to be "getting larger" or "smaller" when doubling or halving their size in one second. Changes of brightness of a 10 degrees spot of light in a dark background were correctly reported as "brighter" or "dimmer." Such changes were frequently perceived as displacements of constant objects in 3-D space. Thus either expanding or brightening spots were described as "coming closer."

Both L. B. and A. A. readily reported the above changes of size or brightness without error for runs of 32 trials in which opposite changes succeeded one another unpredictably. N. G. was less confident and performed short errorless runs in a trancelike state which left her quiet. R. Y. was likewise only accurate in his verbal responses under conditions of exceptional attention when his behaviour was automatic. He complained of tenseness and fatigue. On more than one occasion he gave runs of responses 100 per cent *incorrect*. Thus a variety of verbal responses was obtained; from ready and accurate, to automatic or aphasic replies triggered non-specifically by the stimulus change. As with other tests, the elder two subjects, N. G. and R. Y., showed effects of commissurotomy more strongly than did L. B. and A. A.

L. B. was accurate in discriminating horizontal and vertical orientations of a 10 degrees × 2 degrees black bar when it was brought from the edge to 45 degrees left. When asked to say when to stop the rotation of this bar to make a horizontal or vertical setting, he was accurate to within 5 degrees.

Reports by L. B. and A. A. of the direction of motion of a stimulus were accurate if not more than four directions were to be discriminated (e.g. "up," "down," "to the left," "to the right"). N. G. made many errors when trying to report more than two directions (i.e. she could discriminate "up-down," "in-out," or "near-far"), and R. Y. was able to give significantly accurate runs of reports only for brief periods, even with only two alternative directions.

Illusions reported with changing stimuli recalled the errors of perception that occur in normal far peripheral vision. For example, dim white patterns of light were described as appearing very bright when they were moved suddenly. A circle 2 degrees in diameter expanding slowly to 10 degrees in diameter was said to be "fading out." Faint and blurred shadows were described as becoming dark with sharply defined edges when they were moved. Such responses indicate that the percepts in the left peripheral field were indeed accurately described by the commissurotomy subjects.

(*c*) *Rhythms of motion.*—The subjects were particularly responsive to speed and rhythm of stimuli in the left peripheral field.

When asked to describe the motion of a 5 degrees spot of light and given no further clues, L. B. spontaneously said that 5 degrees/sec was "slow," 20 degrees/sec "pretty fast," and 60 degrees/sec was "fast." Irregular motion inside 2 degrees was called "bouncing about." Sinusoidal displacement horizontally at 2 degrees/sec inside 2 degrees was described as "side to side." He easily discriminated sudden accelerations ("jerking" or "jumping") from "smooth" changes of motion. A. A. also readily reported "quick" *v.* "slow," "smooth" *v.* "jerky" for motion of a 5 degrees light spot. N. G. became very confused when faced with making several alternative descriptions of kind of motion. She could report "quick" and distinguish it from "slow." She discriminated "jerky" from "smooth" with difficulty and became aphasic and distressed in attempting to respond to double questions such as "What kind of movement? and which way did it move?" She made contradictions or irrelevant replies and refused to continue, saying she could not tell or even see the stimulus. Then, again, with simple choice between "quick" and "slow," she responded calmly and correctly. R. Y., characteristically, could not give consistent responses to even simple choices of description for the kind of motion of left field stimuli. Nevertheless, he did correctly report "quick" *v.* "slow" when optimally attentive.

(*d*) *Number.*—When asked to report how many stimuli were in the left field L. B. showed effects of perceptual grouping, and also extinction of the perception of one stimulus when another was moving at a different rate or direction in the field. With 5 degrees black squares separated by 10 degrees and in a fixed configuration he could generally count correctly up to three or four. Correct discrimination of two stimuli close together was facilitated if they were moving relative to each other slightly, but keeping about the same separation.

A. A. accurately said how many stimuli were present up to three or four, showing the same effects of grouping as L. B. This subject (A. A.) has been tested with varying numbers of dots presented tachistoscopically in the left field and was found able to accurately report up to four or five (Nebes, 1971). N. G. correctly reported discrimination of two black rectangles 5 degrees square and 5 degrees apart at 45 degrees left from a rectangle of equal total area. When these two stimuli were alternated unpredictably she correctly said "one" or "two" in an automatic sudden way as each stimulus was presented. She was unable to report large numbers correctly.

(*e*) *Description of shapes and identification of objects by shape.*—In general, L. B. was not able to describe more than one or two distinctive features of stimuli confined to the left peripheral field and his verbal identification of left field forms was poor compared with stimuli of symmetric right field locations. In attempting verbal responses he was frequently confused and he mumbled, or his speech was temporarily arrested. On many occasions he made elaborate and totally inaccurate confabulations describing details of visual appearance which were not even remotely related to the stimuli. Confabulation could be obtained by forcing him to give elaborated

responses, or it could be greatly reduced by cautioning him to give simpler responses, more carefully and slowly. Occasionally, however, he could give a clear spontaneous description of one or two elements of form. Holes or projections in shadows of objects were described and quite fine features of the texture or edge-structure were reported. When two parallel black bars each 1 degree wide and 20 degrees long and with a gap between them of 1·5 degrees were introduced from the left to 45 degrees from the centre, they were described as follows: "straight, like square blocks. No, not square; long and thin, like caskets, two of them." When they were subsequently reduced in size he said that he could see the gap between them at 45 degrees left until it was reduced to 0·5 degree. At this point the lines were 7 degrees long and 0·3 degree in thickness.

Descriptions of left field stimuli made by A. A. were comparable to those of L. B. More complex stimuli gave him difficulty. He said a pyramid was "triangular" and a regular cross he called "square." He could not name a star but said that he definitely knew what it was. A large silhouette shaped like a face of a cat caused him to mumble and complain that he could not think. When prompted he affirmed it was "an animal form."

N. G. said a thin vertical line was a "pencil" and that a square was "not as long" and "a bit wider." She spontaneously reported a cube as "square" but could say no more. A pyramid was "different." More complex forms on the left were not described and she had great difficulty maintaining fixation. R. Y. reported a square as "circular," and described a pair of squares as "two objects." In further tests his spontaneous vocal responses to features of form were considerably less accurate than those of N. G.

(*f*) *Parallax changes.*—Parallactic transformations of shadows cast in the left half of the visual field were made by turning or displacing objects between the point source and the left screen (fig. 7).

L. B. spontaneously described the shadow changes as motion of a solid object. Approach and withdrawal was perceived when a circular hole (a) or a fine wire grid (b) were displaced in-and-out along a line joining the point source and the subject, i.e. along a ray at 45 degrees left in the subject's visual field. L. B. accurately discriminated displacements leading to expansion or

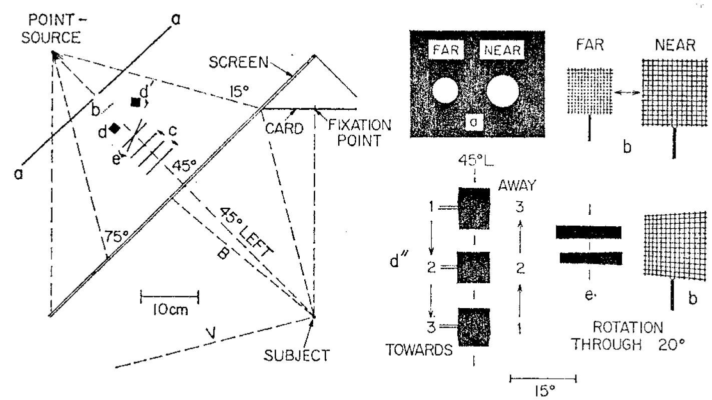

FIG. 7.—Parallactic transformations discriminated in left field and reported verbally. *Left:* Diagram of test field. *Right:* Stimuli.

contraction of a shadow between 10 degrees and 15 degrees in width, the change taking place in 0·5 to one second. This change was equivalent to displacement of an object 1·5 cm wide through 5 cm toward or away from the subject. With a rectangular black bar of tape on a sheet of glass that cast a shadow initially 15 degrees long (c), the minimum change in size of the shadow which the subject reported was an increase or decrease in length of 0·5 degree, equivalent to a 1·5 cm displacement of a 6 cm-long object located at 24 cm from the subject.

Sensitivity to rotations was tested with the grid (b) and with a black cube (d), both of which were mounted on a thin steel tube support, or a rectangle of opaque tape on a sheet of glass (e). Rotation of a 10 degrees shadow of the cube round the 45 degrees left ray was detected, and the direction of rotation correctly discriminated as "clockwise" or "counterclockwise" for rates between 8 degrees/sec and 720 degrees/sec. In 16 trials, with 8 in each direction, he made only one error which he promptly corrected. For rotations at 30 degrees/sec about a vertical axis, L. B. was able to tell the direction of rotation when a thin horizontal rectangular stimulus 20 degrees long and 4 degrees wide, again located at 45 degrees left, was turned through 20 degrees in either direction in one second (e). He distinguished the turning direction by saying which end was coming closer to him, the one toward the front or the one toward the back. With a cube, he had difficulty discriminating the direction of rotation about a vertical axis when the shadow was approximately 5 degrees × 5 degrees at 45 degrees left, but he could do it when this shadow was moved into 30 degrees left (d′). Rotations of the grid (b) were detected when it had turned 20 degrees in 0·5 sec. The grid subtended 15 degrees × 15 degrees and was located at 45 degrees left.

His most impressive performance was with a 6 degrees shadow of a cube rotated about a horizontal axis at right angles to the 45 degrees left ray of his visual field. He was asked to say if the changing shadow, which he said looked like an object turning, looked as if it was rolling "towards" him or rolling "away" from him when he imagined it resting on a horizontal surface. In 10 trials with 5 in each direction he made only one error which he immediately corrected spontaneously. As is shown in fig. 9 (d″), the dimensional changes of the shadow on the screen were a length change of 2 degrees in the vertical direction, and fluctuations in the width over 0·5 degree due to a displacement of the widest point. The information about direction of rotation is carried mainly in the velocity changes at the upper and lower borders, and in the direction which the widest part, corresponding with the nearest edge, moves with respect to the figure as a whole. Clearly L. B. was integrating many small local signals to obtain a unified perception of the direction in which the cube was turning. This sensitivity to combined motion effects with verbal report is most striking considering that he showed very low acuity in his verbal reports for features of static forms or familiar shapes of any kind in the left field. Monitoring and control of gaze fixation throughout these tests was carefully maintained.

None of the other subjects equalled L. B.'s performance in describing these stimuli, though all were highly sensitive to the parallax changes and could report when they took place. None could report any direction of rotation for the 6 degrees shadow of a cube or the 10 degrees wide grid, although reversals of rotation were reported. All subjects could accurately report approach or withdrawal with the larger stimuli (e.g. the grid expanding from 10 degrees to 30 degrees in one second).

(*g*) *Colour.*—All four subjects could accurately report a change of hue in the left field when the luminous intensity was constant. N. G. showed a large autonomic response (galvanic skin potential shift) when a patch of colour (red light) was introduced for the first time into the field at 45 degrees left, without warning (*see* fig. 2). She also exclaimed with excitement but could only guess when asked to name what she had seen.

In discrimination tests for verbal identification of colours, colour shadows in motion in a white surround were obtained by blocking out light from one or two projectors which cast complementary lights on a back-projection screen as described in Methods. A 40 degrees circle of white light centred at 45 degrees left was made by mixing complementary red and green, or blue and yellow and adjusting their brightness to make white. The colour of the filters used in this experiment and the responses of subjects L. B., N. G. and R. Y. are given in Table III.

Each subject was able to report every time a 10 degrees shadow was cast in one of the paired colours to eliminate one complement. With red and green shadows appearing in succession on the left, L. B. first said he saw shadows moving. On the third trial he suddenly noticed that a colour change was involved, but at this stage he failed to identify the colours. In a subsequent run he was given 64 trials, 32 red and 32 green, and asked to say what colour he saw. Though he did not feel sure about his responses, his judgments showed accurate discrimination (Table III).

With 16 blue and 16 yellow in an alternating series he reported blue correctly but gave various responses for yellow. It was verified that he kept his eyes fixated on a black dot on a white card in all the above trials, and that he did not look in the field for a colour match before responding. These results indicate that L. B. could say correctly the approximate colours of red and blue-green stimuli, but that he was not sure about yellow. After the test with blue and yellow he spontaneously reported that the yellow shadow looked redder in the periphery than it did when he looked at it directly. Normal subjects experience a similar effect.

Subjects N. G. and R. Y. performed above chance, but were considerably less accurate than L. B. With the red-green discrimination each made a significant score ($P<0{\cdot}05$) in the choice of "red," "orange" or "yellow" for red, and "green," "blue," "purple" or "uncertain" for green (Table III). Controls for eye fixation on a black dot in the centre of a white card were maintained in all these trials Neither subject gave consistent responses when asked to name colours seen with alternate presentation of blue and yellow. In both the above discrimination tests, R. Y. responded either "blue" or "yellow"; he reported no other colour. N. G. called red "red" or "orange," and green most frequently "blue." The percentage responses of all subjects for the different colours show that blue was the most frequent response, with green and orange infrequent. Subject A. A. reported that he could see colour change in the left field and in a short discrimination test he was accurate in naming blue. No further colour tests were made with this subject.

To eliminate any possible leakage by reflection of sensory information which might give the left "speaking" hemisphere a direct input from the stimuli through the primary input pathway, two further precautions were taken with subject L. B.

The subject was seated as shown in fig. 8, orientated to face a fixation mark at the edge of a rectangular metal screen painted flat-white, and with right eye occluded by an opaque black eye-patch. A 45 degrees circular hole was cut in this screen against which was mounted a back-projection screen. A cone of cardboard, painted matt-black on the inside, was attached on the subject's side of the screen to eliminate all light transmitted from the screen outside the region between the subject's pupil and the screen. The projection path was likewise enclosed in a cylinder of black-painted cardboard. This arrangement prevented light from the screen falling on the bridge of the subject's nose, the right side of the orbit of the left eye, or any other surface in the right half of the visual field of the subject.

Colour stimuli were introduced in the form of strips of Wratten filter material. The same filters were used as in Table III, with the exception that a more transparent yellow (Wratten Filter No. 16, wavelength 589 mμ) was used in place of Filter No. 73. These cast coloured bars 5 degrees in width on the screen. They were inserted horizontally to appear from the left edge of the circular screen which was otherwise uniformly lit with white light. The proportion of coloured light in the whole field was so low that it is highly improbable that the tint of light scattered inside the eye was

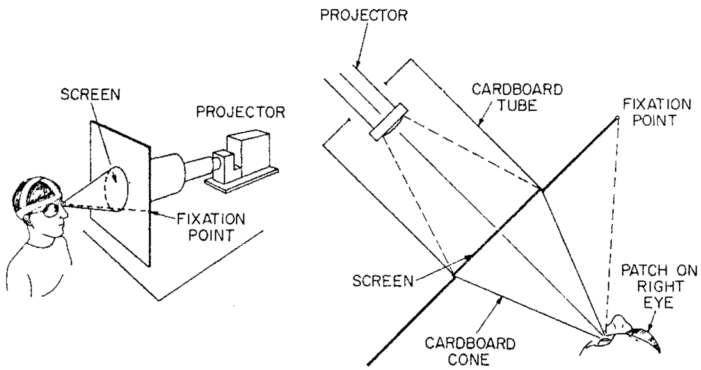

FIG. 8.—Critical colour tests with subject L. B.

sufficiently changed on introduction of the stimulus to permit detection of the colour by stimulation of the left half of the retina. Direct inspection of the screen when diffuse coloured light was introduced in comparable amounts, by inserting the strip of filter so far from the focal point of the projector that an image of the filter was lost, verified that under these conditions discrimination of the colour could not be made.

With these added controls, L. B. continued to make accurate verbal identifications of colour patches appearing in the left field against a white background while he maintained steady fixation. In 32 trials the four colours were given eight times each (Table III). As in the preceding experiment, red, blue, and green were named accurately, although the last two were confused. Yellow was most frequently called orange or light-red, but the responses for this colour were particularly uncertain.

III. Perceptual Rivalry Between Half-fields; Unilateral Neglect

Initial detection of a single stimulus that was moved with prior warning into one field appeared to be as prompt for the left side as for the right, even when the subject was responding vocally. Practice with repeated presentations improved the sensitivity. At this stage, alternating presentation of left and right stimuli or introduction of two equal-sized stimuli at once, one on each side, caused extinction of one or both stimuli.

Surprisingly, all subjects said in some trials that only a left stimulus had appeared, or that the right one vanished when both left and right stimuli were moved at the same time. More commonly, however, the right of two stimuli dominated, and the left was reported to be invisible or weaker. L. B. occasionally reported the left of two equal stimuli to be clearer in outline and brighter than the right. More often he said that he could see the left stimulus clearly enough in the correct position as something bright moving, but that he could make nothing out of its shape or brightness. Once a stimulus had become extinguished either on left or right, it was generally reported to remain unseen for several seconds, even while the experimenter moved it vigorously about.

TABLE III.—RESPONSES TO COLOUR IN THE LEFT FIELD

Colour of stimulus	*Subject*	*Red*	*Orange*	*Yellow*	*Green*	*Blue*	*Purple*	*Uncertain*
Red	L. B.*	28	2	0	0	2	0	0
	N. G.	5	3	1	1	3	1	2
	R. Y.	0	0	10	0	6	0	0
	Totals	33	5	11	1	11	1	2
Green	L. B.*	0	0	0	0	31	0	1
	N. G.	2	1	1	3	6	3	0
	R. Y.	0	0	4	0	12	0	0
	Totals	2	1	5	3	49	3	1
Blue	L. B.	0	0	0	0	13	0	3
	N. G.	0	0	9	0	0	7	0
	R. Y.	0	0	9	0	7	0	0
	Totals	0	0	18	0	20	7	3
Yellow	L. B.	3	2	2	4	3	0	2
	N. G.	0	0	6	0	0	10	0
	R. Y.	0	0	6	0	10	0	0
	Totals	3	2	14	4	13	10	2
% Responses of each colour		12·5	3·5	25	4	40	11	4
Special test; L. B. (8 trials for each colour)								
Red		5	1	0	0	1	0	1
Green		0	0	0	5	3	0	0
Blue		1	0	0	0	7	0	0
Yellow		2	2	1	0	0	1	2
	Totals	8	3	1	5	11	1	3

*L. B. was given 32 trials each of red and green.

Colour	*Wratten Filter No.*	*Dominant Wavelength*
Red	23A	606 mμ
Green	65	501 mμ
Blue	47	470 mμ
Yellow	73	576 mμ

IV. Results with Right Hemidecortication

On May 14, 1966, four years before the present tests, the right hemisphere of G. E., aged 32, was removed by Dr. E. Bechler following identification of a malignant glioma (Bogen, 1969).

The basal ganglia were partially spared. Since the operation G. E. has shown paralysis of the left extremities and is capable only of weak displacements of proximal limb segments in association with trunk movements. She remains alert, sociable and articulate with a tendency to become excited and loquacious in conversation. Her auditory and visual attention seem to be impaired, though once she is engaged in a task or in conversation she tends to be distractable and hyperresponsive.

In tests with the point-source shadow-caster, this subject was unable to report any visual stimuli confined to the left half of the visual field, with the possible exception of a shadow moving between 30 degrees and 60 degrees left of her fixation point which she said looked like something in motion up-and-down the vertical meridian, though no such stimulus was present. Stimuli moving in the right field were reported, but G. E. also exhibited an initial inattention to peripheral right field events, and she required orientating by repeated stimulation before her vigilance reached a level comparable with normal on this her supposedly unaffected side.

In tachistoscopic tests, G. E. showed perceptual completion to the left of her fixation point (Trevarthen, Kinsbourne and Sperry, 1973). She reported that a room looked normal until she was forced to keep her gaze steady and cross-examined about objects entirely within her right field. She then replied that the left half of her field looked blank. Oculomotor tests disclosed that she was able to direct her gaze to the left with movements of her eyes to spoken command or to auditory or somæsthetic stimuli on the left. No evidence was obtained for evocation of leftward reflex eye movements by visual stimuli confined to the left field.

The above tests were performed with the assistance of Dr. Joseph Bogen who was also kind enough to make it possible for G. E. to come to the laboratory.

V. Observations on a Left-handed Commissurotomy Patient, P. D.

This subject, born in 1942, had been an epileptic from childhood. He appears to be inherently left-handed and reports that a number of near relatives show left-handedness. Immediately before operation he had frequent seizures, and he was clumsy, and laboured in his speech, and slow witted, indicating a poor cerebral condition.

Total cerebral commissurotomy was performed in a single operation by Dr. Philip Vogel on November 3, 1969. Drs. Bogen and Saul, who examined him in the immediate post-operative period, report that all voluntary performance and responses to commands were impaired with most loss on the right side (Bogen and Saul, 1970). Occasionally the actions of the two hands were discoordinated, or even conflicting. During the first weeks after the operation P. D. was able to make only a few extremely simple single-word utterances. Such replies to questions as he did give had a latency of one to several seconds. He did, however, show comprehension of simple commands.

The present tests were performed on July 24, 1970, nine months after the operation, through the courtesy of Dr. Ronald Saul of the Los Angeles County Hospital. At this time P. D.'s condition had improved markedly. He could express himself in sentences and reply appropriately to many simple questions. Speech articulation remained poor, however, in spite of speech therapy, and his responses were abnormally slow. He still could not carry out more than the simplest commanded movements with his right hand.

When tested with point-source projection, he reported the movement of shadows in his left field at much higher level than for the right field. For example, he promptly reported all displacements of a shadow moved up or down on the left and he responded correctly to a chance lateral movement, calling it "sideways." For the right field, he signalled appearance or disappearance of stimuli with his right hand, but when asked to say when such events took place, he was unable to speak and he merely winced or pursed his lips. He also showed large galvanic skin responses to these stimuli confined to the right field. On two occasions in 30 trials he was able to say weakly "now," to report that he had seen something on the right.

The spoken responses of this subject were so slow and so awkward that his performance with left-field stimuli may not be compared directly with that of a right-handed commissurotomy subject to right-field stimuli. Nevertheless, it is significant that P. D. could report events for the left field while failing to report comparable events on the right that he could respond to correctly with his right hand. Reversal of lateralization for verbal responses to visual stimuli presented tachistoscopically has been reported for P. D. by Levy, Trevarthen and Sperry (1972).

Discussion

The present findings show that with testing conditions favouring peripheral vision, subjects with cerebral commissurotomy retain a capacity to cross-match stimuli in the two halves of the visual field and to equate and balance left and right

moving contours or boundaries. The same subjects were also able under these test conditions to give crude verbal identification of certain stimuli confined to the left half visual field. Optimal stimuli for the verbal responses were, again, moving or changing effects lasting one second or more. Provided visual attention was adequate, the appearance and disappearance of a dark or a light stimulus, the location in space, or the incidence, direction and speed or rhythmical quality of motion of a stimulus, were correctly reported, as well as its orientation or whether it was elongated or square, single or composed of two parts. Occasionally further outline features were discriminated.

At the same time the present observations confirm prior findings (Gazzaniga, Bogen and Sperry, 1965; Sperry, 1970) that the commissurotomy subject is highly defective in naming or describing stationary objects, patterns, colours, etc., presented exclusively in the left field near the centre. All these same stationary stimuli are easily named when presented at a symmetric location in the right field. A simple object in motion in the far peripheral left field may elicit a prompt and accurate verbal response, but the same left field stimulus shown closer to the fovea tends to cause compulsive orientating responses. Unless the resultant eye movements bring the

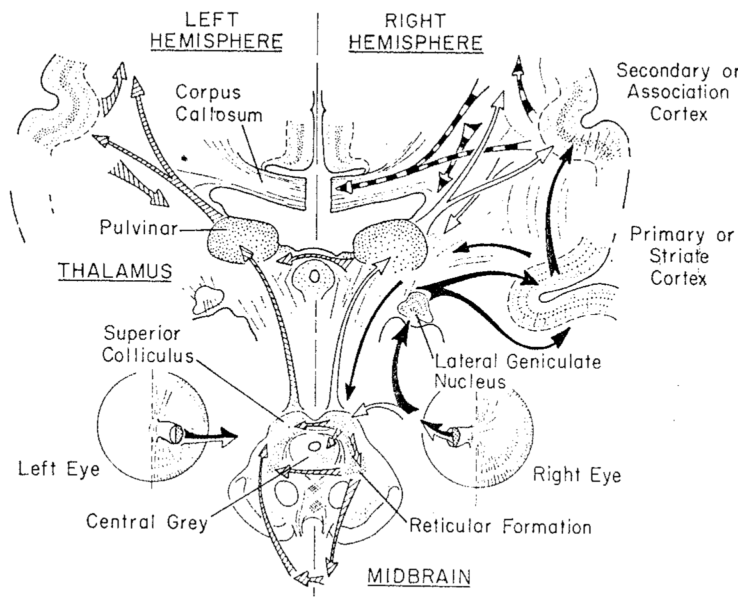

FIG. 9.—Diagram of anatomical connexions underlying unity of ambient vision in commissurotomy subjects. Distribution of input from left visual field. Black arrows: Geniculo-striate input ("focal" input). White arrows: Input from superior colliculus relayed through pulvinar to association cortex ("ambient" input). Black-and-white arrows: Full perceptual information combining "focal" and "ambient" inputs. Cross-hatched arrows: Possible spread of ambient visual information to left side of brain from left half visual field.

stimulus into the right half of the field, the subject will generally deny having seen anything on the left side.

These somewhat paradoxical results support the view put forward recently (Trevarthen, 1968) that there are two levels of visual perception in man and other primates. It appears that when the cerebral hemispheres are disconnected, cross-integration of certain attributes of visual perception of objects in space and their motions are retained in the periphery particularly, as described above, while perception of identity and of detailed features in the central field is divided. Possible pathways to account for the demonstrated ability to talk about left field stimuli and other of the right-left integrations observed are tentatively diagrammed in fig. 9. The essential feature illustrated is the inference that both half-fields of vision are represented in each hemisphere via an extrageniculate visual system relayed through the pulvinar and neighbouring thalamic nuclei from the optic mid-brain centres which receive visual information both from the retina and backstream from the striate cortex (Trevarthen, 1970). The presence of such an extrageniculate visual system is suggested in numerous other lines of evidence, both anatomical and behavioural (Bridgeman and Smith, 1945; Diamond and Hall, 1969; Ebbesson, 1970; Schneider, 1969; Trevarthen, 1968, 1970).

Our observations confirm that removal of the cortex of one hemisphere produces total blindness in the contralateral half of the visual field. In view of evidence for bilateral representation for some visual functions in each hemisphere of commissurotomy subjects, it would appear that hemianopia following ablation of the visual centres of one hemisphere results from removal of corticofugal information essential for visual awareness of stimuli in the affected half-field.

As indicated in fig. 9, the ability of commissurotomy patients to speak about left field stimuli could mean either that the minor hemisphere is able to execute speech under these test conditions, or that the left stimulus was projected into the left hemisphere. Corollary evidence favours the view that the left hemisphere was firmly in control of speech for most trials but that under special conditions some speech was emanating from the minor hemisphere.

Colour naming in these subjects was strongly, but not entirely, lateralized to the left hemisphere. Significant scores obtained with red or orange colours on the left, as contrasted with blue or green, suggest that the ipsilateral or undivided visual projection mediates dichromatic colour perception. Subsequent tests with these subjects seem to confirm that the residual colour naming function for the left half-field is in some respects comparable with that of a dichromat (Trevarthen and Fisher, 1973).

The spontaneous matching of mirror symmetric lines by the commissurotomy subjects is not unlike the mirror interocular effect in perception found in chiasm-sectioned monkeys (Noble, 1966), and in unoperated birds and fish (Mello, 1965; Ingle, 1967) and might be taken to suggest an effect of anatomical bisymmetry of the brain on perception of visual space. Some explanation other than the left-right bisymmetry of callosal connexions cited by Noble is obviously called for in the case of the commissurotomy patients, as with the submammalian forms (*see also* Sperry, 1970).

A strong right-orientating bias in involuntary, presumably disinhibited, eye movements of all subjects, even in tests where all relevant visual stimuli were on the left and continuing when the subjects were showing perceptual neglect of the right half of the display, suggests that visual attention processes are more right-brained for perception of large-scale peripheral stimuli lasting several seconds. This may be correlated with the superiority of the right hemisphere for visual search and recognition with tachistoscopically presented pictures (Levy, Trevarthen and Sperry, 1972). The observed rivalry in perception between left and right fields, with extinction of percepts on one side or the other, gives indication that commissurotomy changes visual attentiveness centrally, introducing abnormal instability of active processes involved in visual consciousness. Evidence was found for a marked overall drop of peripheral visual awareness as a direct and permanent consequence of cutting the cerebral commissures.

The representation and function of the ipsilateral half visual field in each cerebrum is not easily demonstrated under ordinary conditions nor after most types of cerebral pathology. Even more than for auditory and somæsthetic sensibility the ipsilateral system for the more highly discriminatory processes of visual consciousness is far weaker than the contralateral and are easily disrupted and suppressed by the dominant contralateral functions. With mid-line commissure lesions, however, and selective testing procedures that favour ambient peripheral vision the function of these heretofore neglected visual mechanisms becomes evident.

Summary

Long-lasting and changing visual stimuli were used to test peripheral field perception of form, motion and colour in four commissurotomy patients. The stimuli were produced by point-source shadow-casting or by focused projections on large screens surrounding the subjects, and oculomotor fixation was monitored continuously. It was found that appropriately large and "active" stimuli in left and right fields were combined by the subjects into unified percepts which they saw as cross-integrated over the vertical meridian. In addition, they spoke correctly about attributes of similar stimuli that were confined to the left field. These results were obtained while subjects maintained steady central fixation, and in absence of any acts capable of giving non-visual sensory feedback and cross-cueing between the hemispheres.

It is concluded that ambient vision remains undivided after hemisphere deconnexion, in spite of the complete separation of focal visual perceptions at the vertical meridian caused in these same subjects by the operation. A left-handed commissurotomy patient in whom speech was better controlled from the right hemisphere was also examined with the methods described.

Implications of these findings for the anatomy of the central visual system of the brain are discussed with the aid of additional observations on a patient with right cerebral cortex removed surgically.

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THE EFFECT OF NOCICEPTIVE CUTANEOUS STIMULI ON HUMAN MOTONEURONS

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SKIN afferents constitute one of the inputs to alpha motoneurons (MNs), as was early recognized by Sherrington (1898). Studies to date show that these fibres form part of the flexor reflex afferents (Wall, 1970), which in general have an excitatory effect on flexor and an inhibitory effect on extensor MNs.

Investigations in man have supported the results obtained from animal experiments (Hagbarth, 1960). Cutaneous stimuli are usually given during tonic firing of MNs, so that both inhibitory and excitatory effects will be evident (Hoffmann *et al.*, 1948). MN activity is followed by recording muscle action potentials (MAPs). The recording electrodes, whether surface or penetrating ones, in general sample MAPs from a number of simultaneously active motor units (Hagbarth, 1960; Gassel and Ott, 1970). Thus the response of a population of MNs (PMNs) of unknown number is monitored. An analysis of the effect exerted by a peripheral stimulus on a single MN, however, is not possible.

We have used single muscle fibre recording to follow the activity and response of individual MNs. The study had the following aims: to compare the response of a PMN to that of a single MN chosen at random from the same MN pool, to investigate some of the factors underlying the variability of response in a PMN, and to detail the response of single MNs.

It will be shown that there is a marked fluctuation in the response of a PMN. An analysis of the underlying factors indicates that the fluctuations are to be expected and cannot be controlled. The response of SMNs is more stable, and provides added information on the physiology of this reflex arc. Part of this work has been presented in a preliminary communication (Kranz and Adorjani, 1972).

METHODS

The study is based on 23 subjects; 14 men and 9 women, aged 25 to 64 years. Recording was from three muscles, the first dorsal interosseus, the extensor digitorum indicis, and the flexor digitorum profundus, during voluntary isometric contraction.

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