High-Level Motion Processing

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7 Perception of Motion Discontinuities in Patients with Selective Motion Deficits

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Humans can find image discontinuities, which usually correspond to object borders, based solely on motion measurements (Anstis, 1970). This computation is an important component of figure-ground segregation (Gibson et al., 1959; Braddick, 1973, 1980), a fundamental function of the visual system. However, despite the importance of discontinuity extraction, two points are still unclear: What are the visual measurements underlying it? And what is its relationship to the spatial integration of motion signals?

Several theoretical investigators have studied the problem of finding motion discontinuities and its relationship to how the visual system measures velocity (Nakayama and Loomis, 1974; Grzywacz and Yuille, 1990) and integrates motion signals over space and time (Hildreth, 1984; Bülthoff, Little, and Poggio, 1989; Yuille and Grzywacz, 1988, 1989). The proposed theories may be divided into three classes in terms of their hierarchical organization: (1) Discontinuities are computed from direction of optic-flow vectors or spatiotemporal signal measurements (Hildreth, 1984; Grzywacz and Yuille, 1990), but prior to the computation of full optic-flow velocity vectors in relatively localized regions of the image; (2) Discontinuities are computed from the outputs of full local velocity measurement, but prior to a stage that integrates the local vectors to obtain a coherent, global percept of motion (Nakayama and Loomis, 1974; Clocksin, 1980); (3) Discontinuities are computed simultaneously with the motion integration stage (Koch et al., 1989). Common to all these theoretical frameworks is the question of whether the processing of information related to the extraction of discontinuity is hierarchically organized (see also Grossberg, chapter 1; Hildreth and Royden, chapter 9; Yuille and Grzywacz, chapter 6).

Physiological and anatomical studies indicate a degree of hierarchical processing of motion in the cortex (for a review see Maunsell and Newsome, 1987). For example, layer 4b of area V1 (Dow, 1974; Blasdel and Fitzpatrick, 1984) is one of the earliest stages providing an explicit representation of direction of motion at the level of individual neurons, which is then further processed in the middle temporal area (MT) (Zeki, 1969; Maunsell and Van Essen, 1983). It is unclear what cortical area computes visual speed, that is, what area has a speed representation which is independent of spatial and

temporal frequencies. While it might be MT (Newsome, Gizzi, and Movshon, 1983), it is almost certainly not V1 (Tolhurst and Movshon, 1975; Holub and Morton-Gibson, 1981). The spatial integration of motion signals might be performed in MT or in the (later) medial superior temporal area (MST), since these areas tend to have large receptive fields (Gattass and Gross, 1981; Tanaka et al., 1986; Desimone and Ungerleider, 1986; for a review see Tanaka, chapter 10). These functions might also be assigned to other extrastriate areas that process motion.

Psychophysics provides valuable information pertaining to hierarchical processing of motion information in humans. Precise measurements of velocity seem to require spatiotemporal integration (McKee, 1981; McKee and Welch, 1985). Motion discontinuities appear to be computed after some absolute motion measurements are made (Baker and Braddick, 1982; van Doorn and Koenderink, 1982, 1983). Computation of discontinuities has been suggested to involve motion antagonistic mechanisms (Hildreth, 1984) or the exploitation of the population code of directionally selective cells (Grzywacz and Yuille, 1990).

In this paper we take a different approach to test the theoretical proposals on the organization of motion processing underlying discontinuity extraction. We investigate performance on seven psychophysical motion tasks of patients with focal brain lesions involving the neural circuits mediating specific aspects of motion perception. This investigation is complemented by magnetic resonance imaging (MRI) studies, and neurological, neuro-ophthalmological, and neuropsychological evaluations. Such patient studies offer a valuable opportunity to infer the neuroanatomical substrate of specific motion computations in humans and to learn how these computations relate to each other. The results of this study were previously presented in a short form (Vaina et al., 1990a; Vaina and Gryzwacz, 1992).

MATERIALS AND METHODS

Clinical Background of the Patients

The four patients, A.F., C.D., M.S., and O.S., had bilateral brain lesions resulting from cerebrovascular accidents. In all cases, the initial diagnosis was made on the basis of a CT (computed tomography) scan, and neurological signs and symptoms. At the time of our evaluation none of the patients was under antiseizure or psychiatric medications. The patient C.D. was on prophylactic treatment with small doses of Inderal for possible migraine headaches. The lesions involved directly or disconnected anatomical areas believed to mediate visual motion analysis. In order to obtain a more detailed anatomical visualization of the lesion sites, all the patients underwent MRI studies, which were obtained when the lesions were stable. The patients' clinical examinations included neuro-ophthalmological and neuropsychological evaluations, which in all cases occurred within one week of the MRI scan. The neuro-

ophthalmological examinations included quantitative measurements of visual fields by Goldmann perimetry, eye movements, and letter acuity. Contrast sensitivity was assessed both with the clinically used Vistech-6500 chart (Ginsburg, 1983; Vaina et al., 1990c, d) and with a computer-generated contrast sensitivity test which measured contrast for both static and moving sinusoidal gratings varying in spatial frequency from 0.2 cyc/deg to 5 cyc/deg. Color perception was evaluated with the Farnsworth-Munsell 100 hue test (Farnsworth, 1943).

All the patients and age-matched healthy volunteers signed the informed consent form according to the Boston University Human Subjects Committee regulations.

The focus of this study is on the patients' performance on a set of psychophysical motion tasks. Neuropsychological tests, including static control tests summarized in table 7.1, were also administered to determine whether the deficits observed were specific to motion processing. The data on the motion psychophysical tasks reported in this study were obtained in the same time period as the control measurements and the clinical examinations.

The neuropsychological evaluation of the patients included a subset of tests from the Wechsler Adult Intelligence Scale Revised (WAIS-R), Benton lines test for assessment of orientation discrimination abilities, and the dot-counting test for screening for spatial localization deficits. Visual organization was tested with brightness subjective contours (Kanisza, 1976). Patients' ability to recognize objects was assessed using common objects photographed from front view and from noncanonical views (Warringrton and Taylor, 1973). Facial recognition ability was assessed with the Benton face

Table 7.1. Results from the ophthalmologic and neuropsychological tests administered to the four patients. I, impaired; A, absent; N, normal; NA, not administered.

Tests	A.F.	C.D.	O.S.	M.S.
Letter acuity	20/30	16/30	16/30	20/30
Stereovision	I/A	A/A	N/N	N/N
Contrast sensitivity	N	N	N	N
Color vision	N	N	N	N
Visual IQ	104	90	110	100
Performance IQ	68	64	89	66
Spatial relations	I (70%)	I (40%)	N (91.5%)	I (57%)
Benton lines	N.A.	I (43.3%)	I (33.3%)	I (48.5%)
Dots counting	N (100%)	I (55%)	N (100%)	N (100%)
Subjective contours	N	A	N	A
Form discrimination	N (97%)	N (90%)	I (75%)	I (75%)
Object recognition (front views)	N (95%)	I (75%)	N	N
Object recognition (unusual views)	I (53%)	N.A.	N	I (45%)
Face recognition	N (50)	N (49)	I (32)	I (37)

recognition test (Benton et al., 1978). We evaluated the patients' ability to perform visual discriminations of form with the Efron shapes test (Efron, 1968) and their depth perception in tasks of global stereopsis with Julesz's random-dot stereograms (Julesz, 1971) and with the clinical Randot test (Randot stereotests, Stereo Optical Co. Inc., Chicago). We also carried out a more in-depth assessment of spatial localization ability. The results are presented in table 7.1. A detailed description of all these tasks can be found in Vaina (1990) and Vaina et al. (1990b).

Here we will briefly describe only those neuropsychological tests which are not part of the usual battery of clinical neuropsychological evaluation tests.

Form Discrimination Two versions of the Efron shapes test were used. First, a black, two-dimensional figure was displayed on the center of the CRT for 100 msec, and in a yes/no procedure subjects were asked to decide whether the figure was a square or an oblong. The total area subtended by the figure remained constant; the variable parameters were the height and width ratios. Second, the same figures were used under a different presentation mode. In a two-temporal-alternatives choice task, subjects were asked to determine whether the first or the second figure portrayed a square.

Position Discrimination This test (McQuarrie, 1953; Warringrton and James, 1991; Vaina et al., 1990b) addressed the subjects' ability to perceive relative positions of objects in two-dimensional space. The stimulus consisted of two squares displayed simultaneously, side by side. One square contained a small black dot exactly in the center (the standard) and in the other square the black dot was "off-center" (the test). The parameter varied was the offset of the off-center dot (in the test given we used a vertical offset ranging from 8 arcmin to 40 arcmin in steps of two). In a two-alternatives forced-choice procedure and sixty trials, subjects were asked to report in which of the two squares the dot was off-center and whether the off-center dot was above or below the center.

Patients' History

A.F. The patient A.F. is left-handed man, with bilateral lesions due to hypertensive hemorrhagic strokes in April 1988 at age 60. He had no paralysis, although his movements were slow and carried out with caution. He was hesitant and inaccurate in touching objects placed in the reaching distance (more in the left visual field than the right). However, he could clearly see and visually recognize these objects. He was not apraxic and had no language deficits. An MRI study performed in July 1988 showed lesions surrounding the trigones of lateral ventricles (the junction of the occipital and temporal horns with the bodies of the lateral ventricles) bilaterally. The lesion undercuts the temporal-parietal-occipital junction bilaterally. The right hemisphere lesion was larger than that on the left, but both extended dorsally into the posterior parietal lobes (figures 7.1c–7.1f).

Visual field charted by Goldmann perimetry revealed a dense congruous loss of the left inferior visual field bilaterally consistent with the anatomical locus of his right hemisphere lesion. There was also a minimal loss in the upper visual field (figures 7.1a and 7.1b). Letter acuity with correction glasses was 20/30. On the examination of ocular motility, there was no strabismus, and saccadic eye movements to static targets were normal both to the right and left. However, A.F. could not hold fixation in the left lateral gaze and tended to drift back toward the central fixation. He also substituted saccades for smooth pursuits bilaterally when following a smoothly moving target.

The patient's performance was normal on the following psychophysical tasks: contrast sensitivity for orientation gratings; discriminations of form, color and gray levels; and perception of subjective contours. He was, however, unable to perceive form in global and local stereopsis and was impaired on spatial localization. On the WAIS-R, he showed an average Verbal IQ of 104 and a severely depressed Performance IQ of 68. He was severely impaired on visual recognition of objects photographed from noncanonical views (Warrington and Taylor, 1973) and on the Gollin figures task. (A substantial fraction of A.F.'s results presented here appeared elsewhere (Vaina et al., 1990b, 1990c, and Vaina, 1994). We present these data again, because this paper has a different focus than the earlier paper and because here our purpose is to make comparisons across four lesion cases).

C.D. The patient C.D. is a right-handed woman with a history of hysterectomy in July 1988 and estrogen treatment postoperatively. In September 1988, at age 42, she had a major nonhemorrhagic stroke in the territory of the posterior cerebral artery involving bilaterally the primary visual cortex (area 17) and tissue corresponding to the location of areas 18 and 19. The lesion extended slightly into the posterior parietal lobes and the left cerebellar hemisphere. She had a mild left hemiparesis affecting leg more than arm, from which she recovered while in the rehabilitation hospital. On the initial neurological examination in September, C.D. was unable to reach accurately for objects with either hand (and in either visual field). She was unable to track slowly moving visual objects. She reported that she could see the world only "in pieces" and on neurological examination her visual deficits were consistent with simultagnosia (Wolpert, 1924). When looking at an object she would focus on an arbitrary detail but fail to perceive the whole object. For example, when confronted with miniature veridical reproductions of several objects and animals, she could identify them correctly only when the color was a specific, defining attribute (e.g., tiger) or there was a specific part that she happened to focus on. Confronted with a rabbit she said, "long ears, must be a rabbit"; a gray elephant she described as, "It's gray, must be an elephant or a mouse. Oh, it has a long trunk, so it's probably an elephant." She had more difficulties with manmade objects that did not have specific, identifying features; thus, she identified the picture of a pair of wool mittens as "drums." On formal testing she was unable to carry

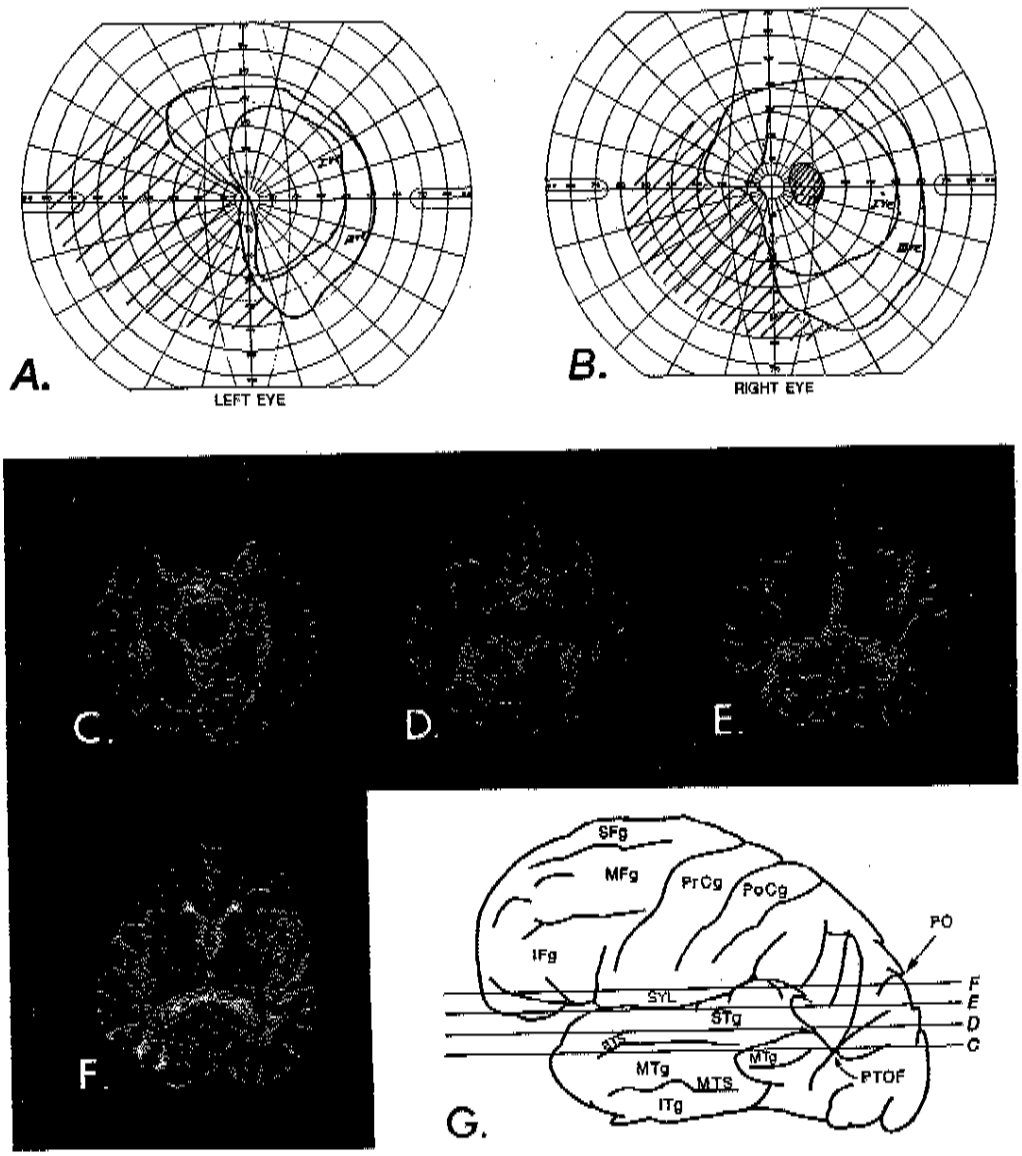
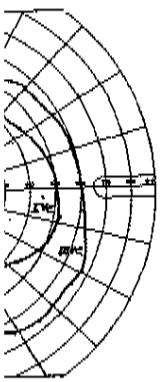
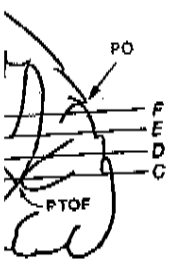


Figure 7.1 Visual fields and magnetic resonance imaging of A.F.'s brain three months following a stroke and the localization of the axial scans on the lateral view of a human brain. (A and B) A.F.'s visual fields by perimetry. A.F. has a bilateral congruous loss of the left inferior visual field and a minimal loss in the upper visual field. (The hatched areas denote field loss and the open areas denote intact filed.) (C, D, E and F) The relevant slices in axial view of T2 weighted magnetic resonance imaging studies (Tr/2000ms/TE80ms) obtained at the Massachusetts General Hospital in Boston. bl, body of the lateral ventricle; h, hemosiderin; fl, frontal lobe; oh, occipital horn of the lateral ventricle; pl, parietal lobe; po, parietal-occipital sulcus; sf, Sylvian fissure; ssc, supersellar cistern; t, trigone of the lateral ventricles; tl, superior temporal gyrus; t2, medial temporal gyrus; ptof, parietotemporo-occipital fossa (see G). (C) The picture shows the temporal horns of the lateral ventricles and some patchy hyperintensities at their margins, more on the right. Areas marked ptof are in the region pointed to on the template (G). (D) the picture shows local tissue loss in the right hemisphere at the sites of the hemorrhagic stroke in the parietal lobe





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out any same-different tasks since she could not see two objects at once. She could do only the version of the Efron shapes test in which only one object was presented at one time. On dot counting she scored at chance (see table 7.1). Also, she was unable to count objects placed in the intact portion of her visual field, could not localize objects in space or plane by sight, and could not perceive depth. She reported that the houses across the street looked so close that she thought she could reach them. She was strikingly impaired on motion perception. For example, she reported that she could not see the second hand of the clock move; she inferred its movement from the change in position. Acuity was reduced to counting fingers at 1 m in both eyes. These deficits interfered significantly with her ability to carry out successfully even the simplest daily tasks.

Several of these abilities were recovered in roughly six weeks after her stroke. Her acuity was found to have improved to 16/30 in each eye, and all the data reported here were obtained after this improvement. She remained severely impaired on depth perception and on spatial localization by sight. She was still impaired on several visual motion tasks. The patient's performance on several neuropsychological tasks was repeated in November 1988 and the results are reported in table 7.1. Her performance was normal on the discrimination of color, form and contrast sensitivity. Surprisingly, when presented with a task of discrimination of direction of motion in moving gratings, her contrast sensitivity score was normal in both the right and the left (the blind) visual field. Her normal results on the form discrimination and position localization tasks, which were of same-different type, together with her now-normal perception of objects, indicate that indeed she had recovered from the simultagnosia. Her depth deficits, however, remained severely impaired; on formal testing, global stereopsis was absent and local stereopsis was 18 SD from normals. Her performance on the spatial localization was in the impaired range, but markedly improved from the previous testing. In the

Figure 7.1 (continued)
just medial to the occipital horn of the lateral ventricle and anterior to the parietal occipital sulcus. There is also some patchy hyperintensity in the temporal lobe along the lateral margin of the right occipital horn. A localized hyperintense area in seen in the left temporal lobe adjacent to the lateral proximal margin of the occipital horn, and some hyperintense areas are seen in the margins of the occipital horn. Images (E) and (F) show bilaterally larger patchy areas of hyperintensity posterior, medial, lateral, and above the trigones and at the margins of the bodies of the lateral ventricles. Tortuous narrow bands of hemosiderin (labeled h) are seen in both images at the site of the recent hemorrhage. (G) A schematic drawing of the adult human brain showing the major gyri and sulci in lateral view. The planes marked by C, D, E, F and correspond to the approximate planes of the images marked by the same letters. IFg, inferior frontal gyrus; ITg, inferior temporal gyrus; Mfg -middle frontal gyrus; MTg: middle temporal gyrus; PoCg, postcentral gyrus; PrCg, precentral gyrus; SFg, superior frontal gyrus; STg, superior temporal gyrus; STs, superior temporal sulcus; MTS, middle temporal sulcus; PO, parietal occipital sulcus; SYL, Sylvian fissure; and PTOF, the parietotemporo-occipital fossa from Polyak (1957, figure 271), which several authors suggested correspond to the human homologue of the macaque MT. The horizontal lines correspond to the levels of the axial scans corresponding to (C, D, E, F).

positioned discrimination task she accurately reported offsets of 20 arcmin or larger. Dot counting remained impaired. Her score on the perception of subjective contours task was at chance level. At this time C.D.'s scores on the WAIS-R were in the average range for the Verbal IQ (90) and very impaired on the Performance IQ (64). She scored in the normal range on the Benton facial recognition test.

In parallel (November 1988) we also obtained an MRI study of her brain and neuro-ophthalmological evaluation. The MRI showed a large right occipital pole infarct and a smaller area of infarction in the left occipital region (figure 7.2). The lesions involve partially the primary visual cortex, lateral portions of areas 18 and 19 bilaterally, and in the right hemisphere, the lesion extended into the middle and upper portions of the inferior temporal gyrus and the posterior parietal lobe (figure 7.2c, d, e, f). The neuro-ophthalmological examination revealed a bilateral homonymous hemianopia, more pronounced on the left than on the right side (figure 7.2a and b). The patient had good convergence and no nystagmus in any visual field. Eye movements in the right visual field were normal and, surprisingly, in the blind left field, she had jerky movements to the stimulus, suggesting that vision was not completely absent (although, as we shall see further, on formal testing in the blind field she was not aware of distinguishing any stimuli, moving or static).

M.S. The patient M.S. is a right-handed woman who had a history of migraine headaches prior to a cerebrovascular accident in December 1987 at age 42. She had a transient cortical blindness which resolved in a few days. Initial CT scan and lumbar puncture were both negative. She had no paralysis, speech difficulties, or apraxia. She had marked difficulties with coordination, which resolved over a few months' period. Secondary to visual problems, she was unable to read, balance her checkbook, write on a straight line, or drive a car. She reported that she was afraid to cross a street with busy traffic, because she had difficulties seeing how fast cars were approaching.

Because of no significant diagnosis she was initially placed in a psychiatric hospital and was treated for depression. As her visual symptoms did not improve, in May 1988, she underwent MRI studies (figure 7.3c, d, e, f, g), which revealed bilateral occipital lobe infarcts, including the tips of the occipital poles. In the right hemisphere, the lesion extended upward and laterally into the inferior occipital-temporal gyrus, and into the posterior medial-temporal gyrus, to the trigone of the lateral ventricle. The left hemisphere lesion was smaller and mostly subcortical, extending to the margins of the trigone of the lateral ventricle. The lesion also involved both posterior lateral parietal lobes. A small lesion was seen in the left cerebellar hemisphere. Neuro-ophthalmological examination done at that time was normal except for her visual field (figure 7.3a and b), which showed scotomas consistent with the lesion in the left occipital pole. Visual acuity was 20/40 in the left

eye and 20/50 in the right eye. With both eyes her visual acuity was reliably 20/30.

She was referred to a rehabilitation unit for comprehensive evaluation of her perceptual deficits and for neuropsychological evaluation. Her scores on the WAIS-R were in average range for Verbal IQ (100) and in severely impaired range for Performance IQ (66). She scored in normal range on the Benton facial recognition test.

Table 7.1 shows that M.S.'s performance was normal on contrast sensitivity for orientation, and for the discrimination of color and form. Global and local stereopsis were also normal. She was impaired on the position discrimination task (for vertical offsets less than 20 arcmin) and failed to perceive subjective contours.

O.S. The patient O.S. is a right-handed man with a past history of hypertension, coronary bypass surgery, and a bilateral occipital stroke in 1985 at age 72. This resulted in a severe visual field loss. MRI studies (figure 7.4c, d, e, f) were performed in 1989 and showed bilateral tissue loss in the medial inferior portions of the occipital lobes also involving the primary visual cortex, a small portion of area 18, and extending medially to the occipital horns of the lateral ventricles. In the left hemisphere, the lesion extended forward between the margins of the tentorium and the proximal portion of the occipital horn of the lateral ventricle. The lesions also slightly involved the posterior portion of the temporal lobes.

The results of the neuro-ophthalmological examination were remarkable for severe visual loss in both visual fields, with only a preservation of the inferior temporal crescent in the left eye, which suggested that the infarction extended further rostrally in the left occipital lobe than the right (figure 7.4a and b). Uncorrected visual acuity was 20/30 in both eyes.

Neuropsychological evaluation showed on the WAIS-R a high Verbal IQ score of 110 and a Performance IQ of 89. Overall, the tests results indicated good cognitive and intellectual abilities. O.S. was very impaired on tasks of drawing familiar objects from memory, but could copy drawings of those objects. His scores on the Benton facial recognition test were in the impaired range, although he did not spontaneously complain of failing to recognize faces. His performance was normal on tasks of discrimination of contrast, form, and color. Global and local stereopsis, position discrimination, and perception of subjective contours were normal.

VISUAL MOTION PERCEPTION

The reasons for including the four patients in this study were their good contrast sensitivity, good performances on static psychophysical tasks (except on the spatial localization on which they were impaired), and their poor performances on visual motion tasks.

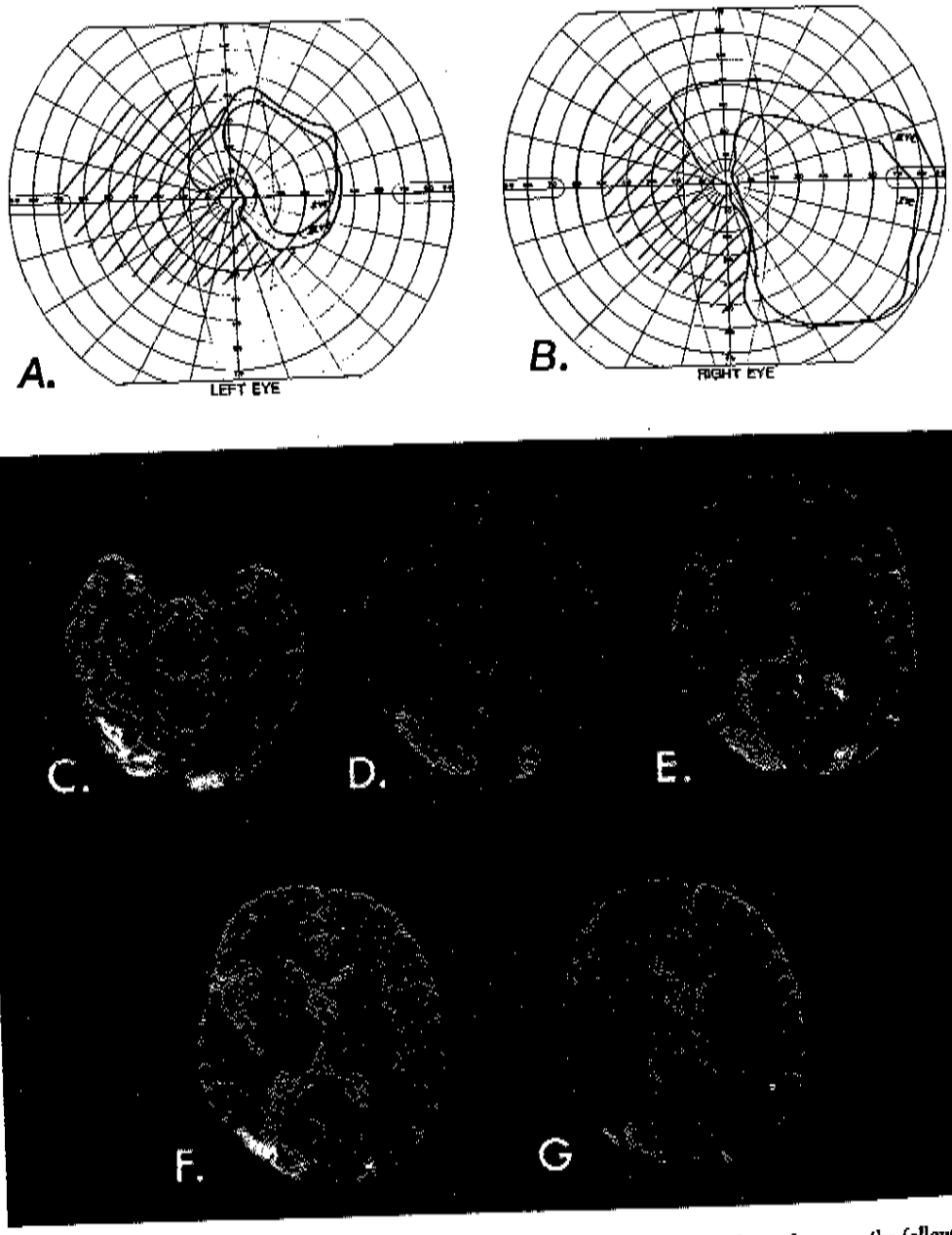
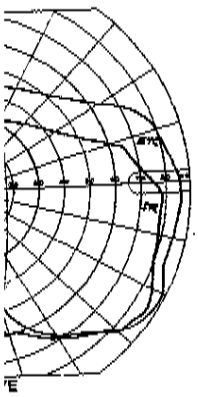


Figure 7.2 Visual fields magnetic resonance imaging of C.D.'s brain four months following a hemorrhagic stroke and the localization of the axial scans on the lateral view of a human brain. The labeling is same as in figure 7.1. (A and B) C.D.'s visual fields by perimetry. The patient has left inferior field loss in both eyes. There is also a right homonomous inferior field loss. An MRI was performed on a 0.3 Fonar unit at the Somerset Imaging Center. Six millimeters thick T-2 (2183/85 TE/TR) axial images were obtained throughout the brain. (C, D, E, F, and G) Infarcts in the occipital lobes bilaterally involving partially the area 17 and more substantially the areas 18 and 19. Images (C, D, E, and F) show that the lesion in the right hemisphere extends from the lower posterior portion of the occipital lobe with the junction with the middle and upper portions of the middle temporal gyri. (E) The central portion of the lesion extends up b



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This section describes six psychophysical motion tasks. The first two tests are controls to show that the patients did not have basic problems with perceiving two-dimensional form, detecting spatial inhomogeneities in optic flows, and discriminating direction of motion. The third and fourth experiments show that some patients could not localize discontinuities and perceive two-dimensional shapes defined by sharp gradients in direction or speed of motion. Solving these tasks requires detection of gradients, a local (not integrative) computation. Finally, the fifth and sixth experiments address visual functions that might require integration of basic measurements: local speed (which might require integration of spatiotemporal-frequency measurements) and global motion (which might require spatial integration of motion).

Apparatus and Method

All stimuli were generated and presented, and responses collected and analyzed, using a Macintosh IIcx computer with an extended 8-bit video card. The stimuli were presented in the center of the Macintosh standard RGB monitor with a resolution of 640-pixel-by-480-pixel, a frequency of vertical retrace interrupt of 66.7 Hz, and P4 white phosphor. Random dots were used to minimize position cues and to isolate motion mechanisms (Nakayama and Tyler, 1981). In all experiments, each picture element (pixel) subtended 1.8×1.8 arcmin at the viewing distance of 65 cm. The background of the display was black and the random dots were painted white. The patients and control subjects viewed the display binocularly in a darkened room. The subjects were first familiarized with the display and task, through examples and feedback. Feedback was not provided during the experimental sessions. To repeat a trial the subject pressed a specially designated key on the computer keyboard. The interval between two trials was maintained at constant 1 s during which the screen was black.

The only source of illumination in the room was that reflected from the computer screen. The luminance of the displays, measured with a photo spotmeter (PR1510, Kollmorgreen Corp., 1985), in experiments 1 through 4, was 22 cd/m^2; in experiment 5 it was 0.13 cd/m^2; and in experiment 6 it was 0.6 cd/m^2. The observer was instructed to restrict fixation to the center of the screen. The control group consisted of normal volunteers with no known ophthalmologic, neurological, or psychiatric disorders, and they were matched by age with the patients (their ages ranging from 45 to 70 years). All the subjects were inexperienced as observers in psychophysical tests. All the normal subjects had corrected-to-normal vision.

Figure 7.2 (continued)
the lateral margin of the trigone of the occipital horn of the lateral ventricle and it extends superiorly into the posterior medial margin of the parietal lobe (F) and (G). Images (C-G) show that the lesion in the left hemisphere is smaller, involving the occipital pole, and it extends slightly into the lower temporal region and along the medial margin of the parietal region.

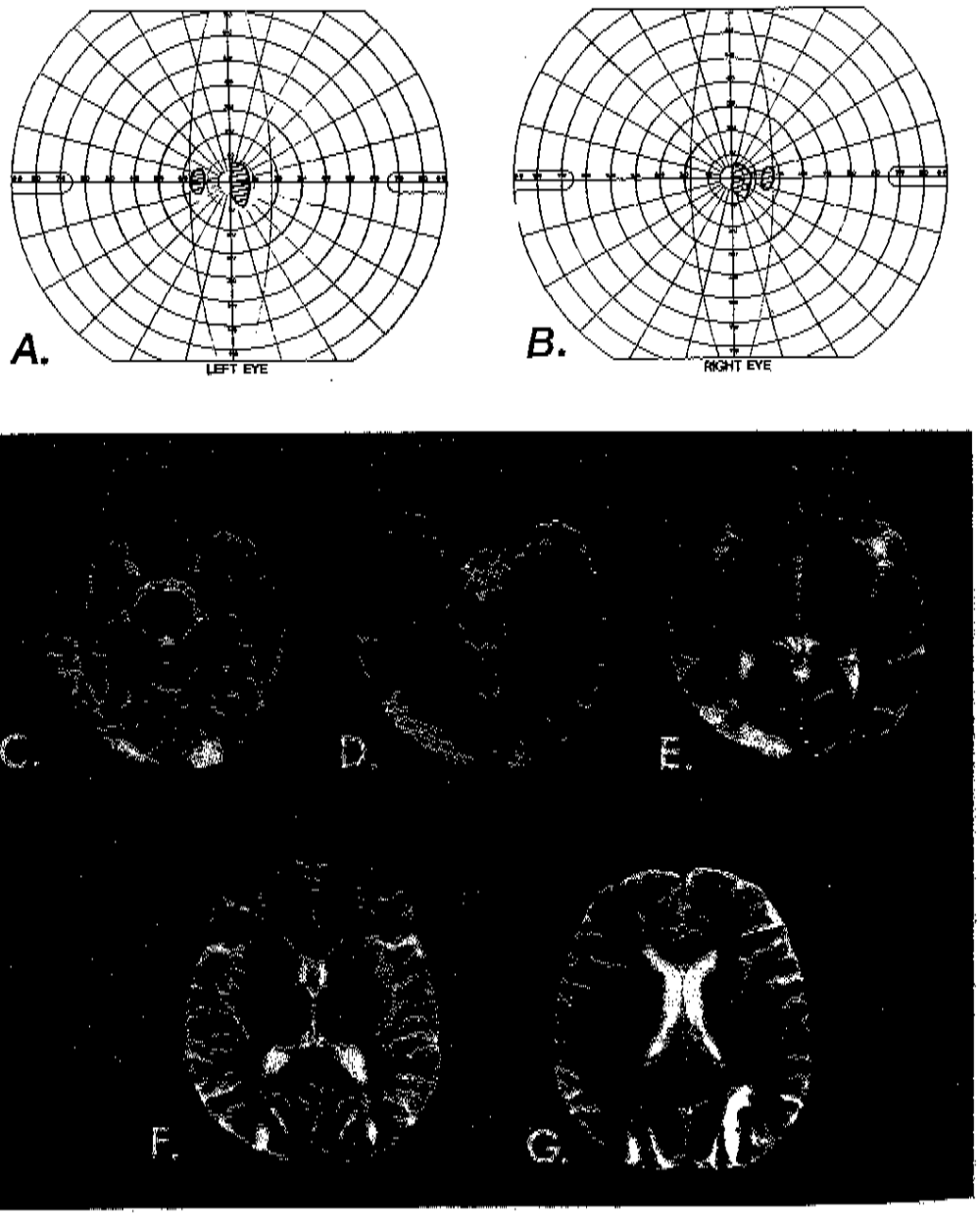
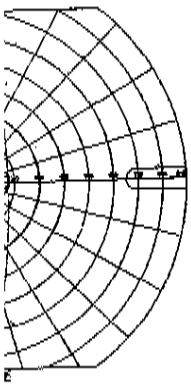


Figure 7.3 Visual fields and magnetic resonance imaging of M.S.'s brain three months following a stroke and the localization of the axial scans on the lateral view of a human brain. The labeling is same as in figure 7.1. (A and B) M.S.'s visual fields by perimetry. The fields show a paracentral congruous right homonymous defect suggesting a lesion in the tip of the left occipital lobe. An MRI study was performed on a 1.0 Magneton unit at the New England Medical Center. Images are 8 mm thick with a 2.4 mm gap between slices. Images (C–G) show axial T2 (2500/80/40 TR/TE) slices. The lesions involve bilaterally the occipital lobes including partially the area 17 and the tip of the occipital poles, and extend into areas 18 and 19. In the right hemisphere the lesion also involves directly the junction of the areas 37 and 39. Images (D) and (E)



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and 39. Images (D) and (E)

Experiment 1: Two-Dimensional Form from Motion in a Static Background

The sensation of two moving, planar, simple geometrical forms was elicited by two moving patches of contiguous random dots uniformly displaced from one frame to the next in translational motion across a stationary random-dot display (figure 7.5a). The forms were defined solely by the displacement of each moving patch relative to the static surround. Each of the moving patches had one of the following shapes: square, circle, triangle, cross, or rectangle (oriented horizontally or vertically). The square, circle, and cross had roughly the same area, and the area of the rectangle was half of the square's. The entire display subtended 10-×-10 degrees, and each of the two moving forms covered an area of approximately 2.2-×-2.2 degrees of visual angle. The speed of motion was roughly 3 degrees per second. This displacement gave a vivid impression of two forms translating in opposite directions across the static random-dot background. The interstimulus interval between two consecutive frames was about 30 milliseconds which was sufficient to elicit a smooth percept of motion (Braddick, 1980). This was a same-different task in which the subject was required to fixate a black fixation mark placed in the center of the display and determine whether the two moving shapes were the same. The test consisted of forty trials. (For the subject C.D. and three controls, we repeated the test with only one form moving, and subjects were asked to verbally report the shape of the moving object. Since the results did not differ from the test described, we will report only on the basic test.)

There were two conditions in this experiment. In the first, *form-from-simple translation*, the perception of the two moving forms resulted solely from the displacement of the two patches of dots by a constant horizontal displacement between two consecutive frames. *Form-from-twinkling-motion*, only the dots delineating the contours of the figures were horizontally displaced by a constant amount from one frame to the next. They were randomly repositioned on the contour, thereby eliminating any local luminance cues. This gave the impression of two forms defined by twinkling borders translating across the screen.

Figure 7.3 (continued)
show that in the right hemisphere the lesion extends along the lateral inferior occipital-temporal gyrus and the medial temporal gyrus and further in the posterior parietal lobe. The lesion on the right involves the occipital-temporal-parietal junction. (F) and (G) show two smaller lesions in the left occipital lobe. The lower lesion is larger (but smaller than the corresponding lesion in the right hemisphere) and involves the posterior medial portion of the occipital lobe. A second lesion is seen in (F), which involves the lateral portion of the occipital lobe extending from the posterior margin of the hemisphere anteriorly to the posterior margin of the occipital horn of the lateral ventricle and superiorly into the parietal lobe posterior to the body of the lateral ventricle.

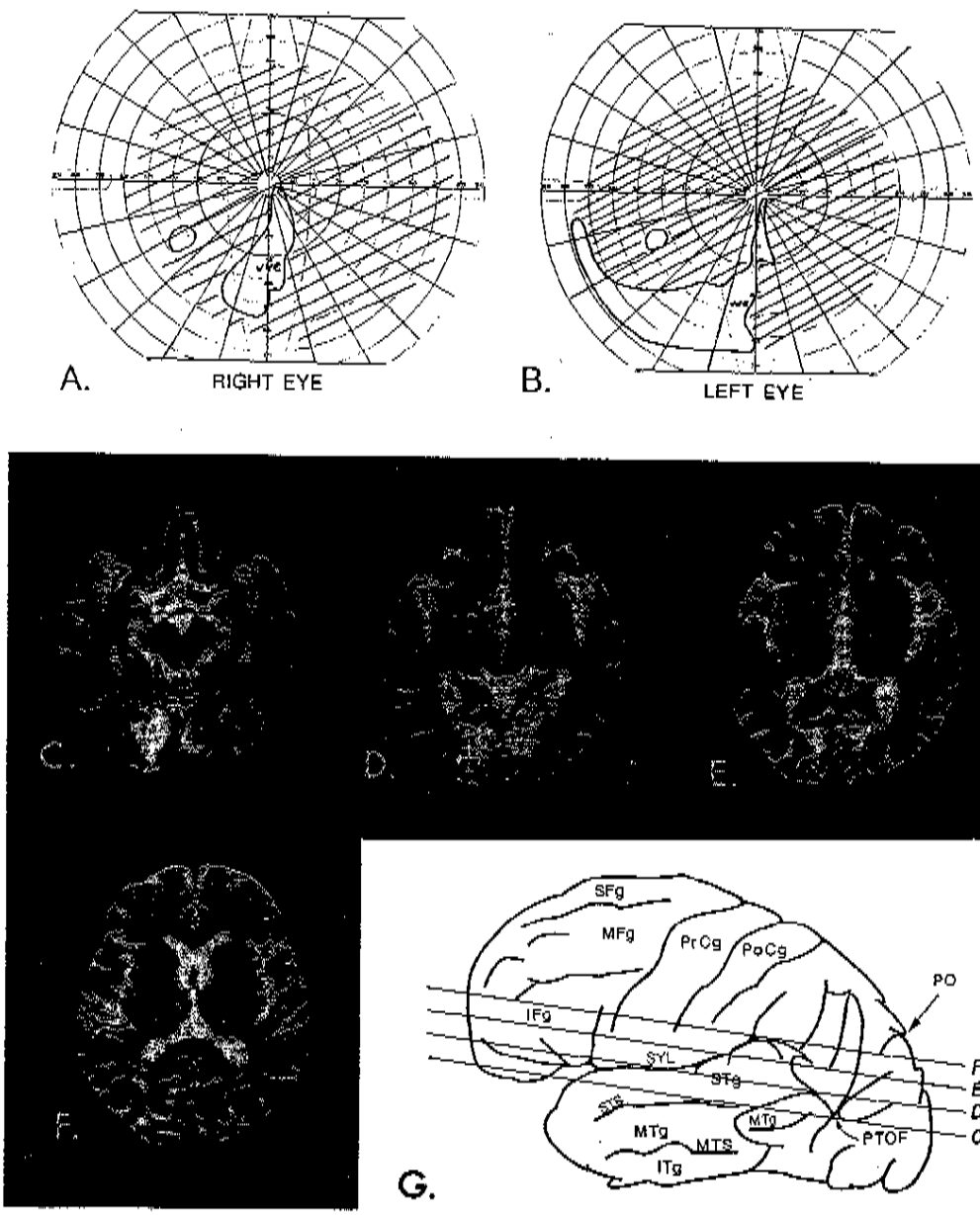
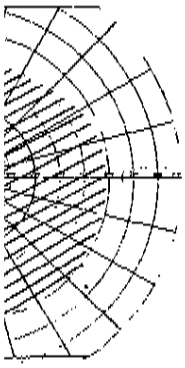


Figure 7.4 Visual fields magnetic resonance imaging of O.S.'s brain three years following a stroke and the localization of the axial scans on the lateral view of a human brain. (A and B) O.S.'s visual fields by perimetry. O.S. has a bilateral visual field loss, more pronounced in the right field than in the left. There is preservation of the inferior unpaired temporal crescent in the left eye, suggestion that the lesion goes further forward in the left hemisphere than in the right. The images (C, D, E and F) are the relevant 5-mm-thick slices in axial view of T2 weighted magnetic resonance imaging studies (Tr/2500ms and TE80ms). The MRI study was performed on a 1.5-T GE Signa unit at the Cambridge MRI center. The labeling is same as in figure 7.1. Images (C–E) show hyperintense lesions, consistent with infarcts, in both occipital lobes involving large portions of the area 17 and portions of the area 18, much more extensively in the right



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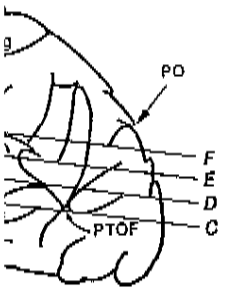

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Figure 7.5b and c shows the performance on *form-from-motion tasks* of the four patients and seven control observers. Figure 7.5b shows the performance on the form-from-simple-translation task of the four patients and seven control observers. The perception of the two moving forms resulted solely from the displacement of the two patches of dots by a constant horizontal displacement between two consecutive frames. All the subjects performed within normal limits (figure 7.5b). There was no statistically significant difference between any of the patients' performances and that of the normal controls, although C.D. and M.S. scored just in the lower limit of the normal control group. Because all the patients could discriminate form from simple translation, and because they could discriminate static forms (the Efron shapes task), it is likely that A.F., C.D., O.S., and M.S did not have a deficit with form discrimination per se.

In the form-from-twinkling-motion task, the twinkling resulted from random reversal of contrast of the dots delineating the shape. That is, there was no consistent correspondence from frame to frame between dots' luminance, which means that the first-order, Fourier, motion detectors could not be used to detect this motion. The twinkling motion is detected by a second-order mechanism, non-Fourier motion (Chubb and Sperling, 1989; Albright, 1992; also see Sato, 1997). Several recent studies aimed directly at comparing first- and second-order motion perceptual abilities in patients with focal lesions (Vaina and Cowey, 1996; Plant et al., 1993) demonstrated that they can be selectively impaired by the lesions. This is consistent with the data presented here. Indeed, patients A.F. and O.S. scored just above chance on the form-from-twinkling-motion task, and during the test they often commented that they didn't see anything "really." It is likely that both these patients failed to perceive reliably non-Fourier motion. On the other hand, C.D.'s performance was within normal limits, and M.S. was only slightly impaired on this task.

Experiment 2: Detection of Motion Inhomogeneity

The display presented a dynamic random-dot field viewed through a square aperture subtending 8 × 8 degrees of visual angle. In any given trial, a sequence of frames was constructed in such a way that either all the dots moved together upward or downward, or the display was divided by a

Figure 7.4 (continued)
hemisphere. The lesions involve the inferior and medial portions of the occipital lobes. In both hemispheres the lesions involve the lower portions of the primary visual cortex and extend, particularly in the right hemisphere, into the regions of the trigones of the lateral ventricles. The lesion in the left extends further forward between the margins of the tentorium and the proximal portions of the occipital horn of the lateral ventricle. Small bright T2 foci are present in the white matter of the hemispheres and in the thalami (F), and in the bodies of the lateral ventricles (G). The picture shows the approximate location and orientation of the MRI image planes shown in (C–E).

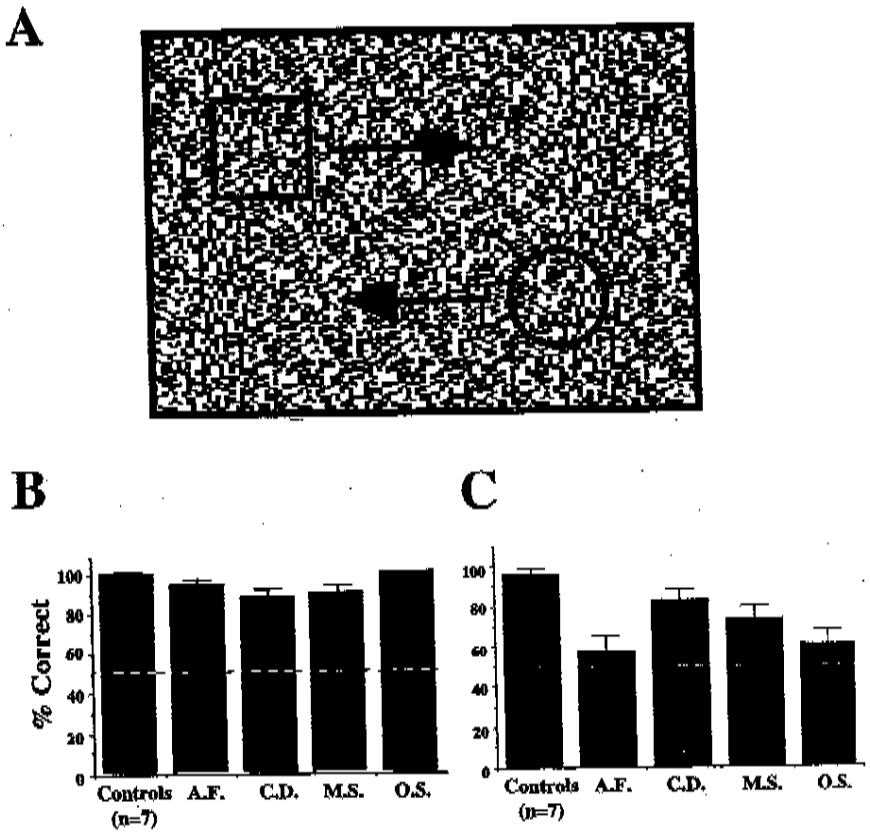
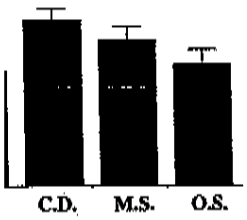


Figure 7.5 Two-dimensional form from motion in a static background. (A) Illustration of the stimulus: The display presented in a 10° × 10° aperture consisted of random dot pattern resulting from 50% black and 50% white dots. Pixel size is 2 arcmin at a viewing distance of 60 cm. A sequence of frames was constructed in such a way that the display shows two patches of contiguous dots coherently translated across the static background with equal speeds. The observer's task was to determine in a two-alternative, forced-choice task whether the two translating two-dimensional shapes were the same or different. There were tow conditions of the task: (1) Form-from-simple-translation (B) in which the forms resulted from the displacement of two contiguous patches of random dots. (2) Form-from-twinkling-motion (C) in which the translating forms resulted from the translation of two twinkling borders. (B) Responses of control subjects and the patients on the form-from-simple-translation. The graph shows the mean percentage of correct responses and error bars for A.F., C.D., M.S., and O.S., and mean percentage of correct responses and standard deviations for seven normal observers. All the subjects performed well. (C) Responses of control subjects and the patients on the form-from-twinkling-motion: The graph shows the mean percentage of correct response and error bars and standard deviations for seven normal observers and the four patients. The scores of O.S. and A.F. were statistically significantly below those of the seven normal controls and of C.D. and M.S.



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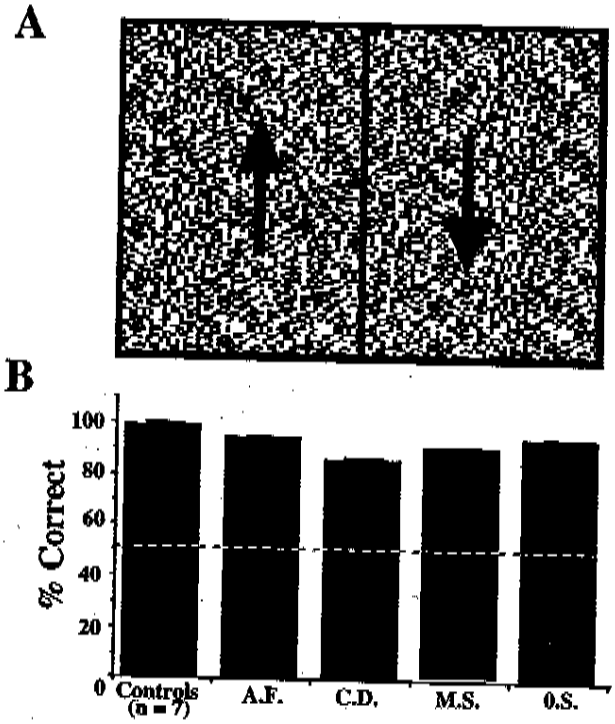

Figure 7.6 Detection of motion inhomogeneity. (A) Illustration of the stimulus. The display consisted of a dynamic dense random-dot pattern (identical to the pattern described in figure 7.5A) presented for 500 msec within a 8° × 8° aperture. In 50% of the trials there was a discontinuity in the velocity field along an imaginary vertical line whose horizontal position varied within 1° from one trial to the next. The black arrows in (A) exemplify the different directions of motion in a trial. In the other 50% of the trials the motion was homogeneous, up or down. The task of the observer was to detect the motion inhomogeneity in a two-alternative, forced-choice procedure. (B) Responses of control subjects and the patients, mean correct responses for each of the four patients and seven age-matched controls. The dotted line indicates the statistical chance responses at 50%. All the patients scored well above chance.

vertical imaginary boundary into two regions where the dots moved in opposite directions. The imaginary boundary originated at random positions on the horizontal axis of the aperture. The entire random-dot pattern was shifted by roughly 9 arcmin between two consecutive frames, which resulted in an average speed of roughly 3°/sec. A conventional wraparound scheme was used, in which dots displaced beyond the boundary of the aperture in the next frame reappeared on the opposite side. The stimulus was on for 500 ms and chance performance was 50 percent correct. This was a two-alternatives, forced-choice task, in which the subject was required to determine whether the motion of the random-dot field within the aperture was homogeneous. Figure 7.6B shows the mean correct responses for each of the four subjects and a group of seven normal subjects (thirty trials). Except for C.D., the patients' performance was not statistically significantly different from the

performance of the normal control group. But even for C.D., the performance was significantly above chance. Thus, this experiment indicates that the patients could detect motion inhomogeneity. Moreover, since the only cue for inhomogeneity lay in the directions of motion, it suggests that all four patients could detect large directional differences.

Experiment 3: Localization of Discontinuities

Subsequently we addressed a more difficult problem in which the subjects had to localize the position of discontinuities defined by relative direction of motion. The stimuli (similar to those used by Hildreth, 1984) were dense, dynamic random-dot patterns subtending 8 × 8 degrees of visual angle. In a manner identical to the previous experiment, a sequence of frames was constructed and the speed of motion was constantly held at roughly 3°/sec. The display was constructed in such a way that there was a discontinuity in the velocity field along a vertical line (figure 7.7a). Along the side there was a 1.4 × 1.4-degree notch (see figure 7.7a), whose distance from the point of fixation varied along the vertical axis from trial to trial, but which remained within only 2 degrees of visual angle from the black fixation mark. The vertical boundary and the notch were entirely defined by the difference in direction of motion between the left and right of the boundary and were not visible in any static frame. Six angular differences (0, 18, 31, 45, 90, and 180 degrees) were used. Each displacement was performed in one screen refresh and was synchronized with the screen to reduce flicker. In this procedure, flicker was not completely eliminated, since at 0-degree angular difference the notch was still visible, as if it were a twinkling border. A possible explanation for this apparent flicker is that the dots inside the notch had shorter lifetimes and thus were turned on and off at a higher temporal frequency.

The test started with a static display of the random-dots aperture, which had at its center a black fixation mark. Subjects were instructed to maintain fixation on the mark. On the subjects' signal, the additional frames appeared one after another. The experimental session consisted of twenty trials for each condition tested. This was a two-alternatives, forced-choice task with the method of constant stimuli, in which the subject was required to determine whether the notch was above or below the fixation mark.

Figure 7.7b shows that the normal subjects performed the task essentially without error for all conditions. (There was no statistically significant difference between the results obtained with the left or right fixation, so the results are pulled together.) The patients A.F., M.S., and C.D performed at chance in the pure temporal-frequency condition (0° angle), thus indicating that they could not use this cue well enough to localize discontinuities (the notch). However, O.S. scored 85 percent in the temporal-frequency condition, which was close to the normal range. A possible explanation for the discrepancy between O.S.'s good performance here and his poor perfor

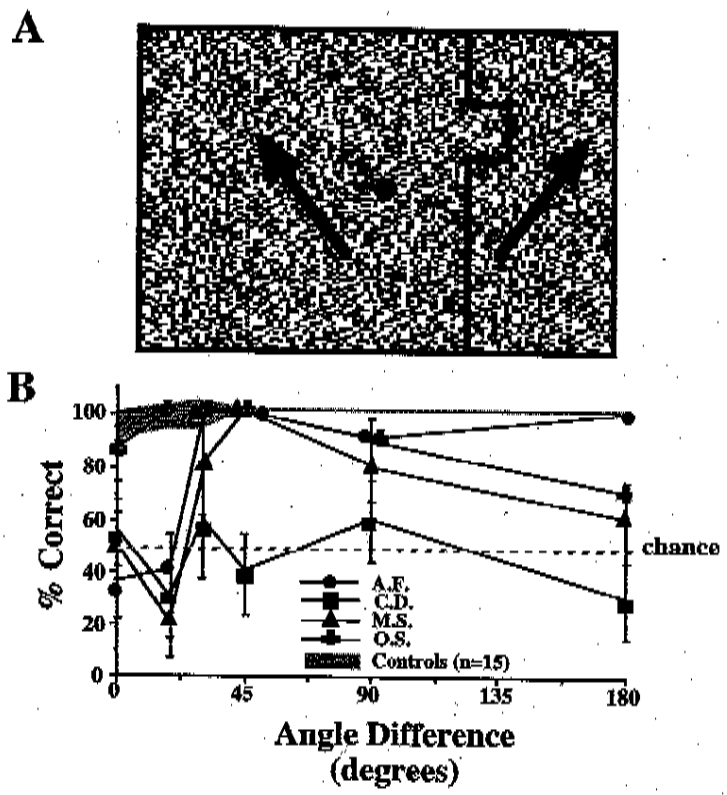

Figure 7.7 Localization of discontinuities. (A) Illustration of the stimulus. The random-dot pattern characteristics are the same as those in figure 7.5A. The differential movement of the two adjacent areas of the pattern reveals a boundary with a rectangular notch defined solely by angle of differences in the directions of motions of the two areas. The position of the notch and of the invisible dividing line between the two areas in relative motion varies randomly within 1° on the horizontal axis. The heavy square indicates the fixation mark. (B) Responses of control subjects and the patients. Percent correct responses for correctly identifying the location of the notch (above or below the fixation mark) for the following angular differences between the two areas: 0°, 18.4°, 37.1°, 90°, and 180°. The line graphs and error bars indicate the percentage of correct responses of A.F., C.D., M.S., and O.S. for these angular differences. The angular difference noted with 0° presents the results on the test condition when the notch is perceived only on the basis of temporal frequency differences between the motions of the two adjacent areas. The hatched area indicates the percentage of correct responses of the control group ± one standard deviation obtained under identical conditions.

mance in the form-from-twinkling-motion task is that inability to perceive non-Fourier motion does not imply impaired low temporal-frequency perception (the dots appeared and disappeared in roughly 750 ms). The scores of O.S. were entirely in the normal range. Another possibility that cannot be ruled out is that O.S.'s deficits are due to some difficulty in detecting outlines as opposed to solid shapes, as would happen if he lost some of the small receptive fields, which is entirely possible given the anatomical locus of his lesion. Patient A.F. scored in the perfect or near-perfect range for the larger

angular differences (31° or more were sufficient to perform an accurate boundary localization). As such, these results indicate that delineation of image regions by relative motion was essentially intact in these two patients, except for small difference in directions in the case of A.F. The patient C.D., on the other hand, was unable to perform the task. She failed to perceive discontinuity in the motion display, even at the largest angular differences. Figure 7.7b shows that M.S. was also severely impaired on this task. It is unlikely that the patients' deficits can be explained by a deficit on spatial localization. Although they were impaired on the spatial localization task, their errors were smaller than 1° of visual angle, and in 75 percent of the trials the notch was positioned between 1 and 2 degrees of visual angle above or below the fixation mark. This was in the range of the spatial resolution of all the patients. In all cases it made no difference whether the notch was presented on the left or the right side of the fixation mark.

Experiment 4: Two-Dimensional Form-from-Speed Differences

A more difficult motion task is that which requires a comparison of speeds without any difference in direction. Speed of motion is encoded with three to four times less precision than direction of motion (for a review see Nakayama, 1985). We employed a task in which observers were required to discriminate two-dimensional shapes from speed differences alone.

An example of the display is portrayed in figure 7.8a. In each trial, the figure subtended an area of roughly 2×2 degrees, and it was randomly positioned within a 6×3.75-degree rectangular aperture of dense random-dots pattern. Both the figure and the background were displaced in the same direction but with different speeds. In 60 percent of the trials, the background speed (displacement of 3.6 arcmin between two frames) was slower than the figure, and in 40 percent of the trials, the background was faster (displacement of 8 arcmin between frames) than the figure. The speed ratios between the figure and the background, using as a reference the speed of the background, had the following values: 3, 2, 3/2, 2/3, and 1/2. In all trials, the interframe interval was roughly 60 milliseconds, which was sufficient to elicit a smooth percept of motion.

The method of constant stimuli was used and observers were asked to make a six-alternative, forced-choice judgment indicating which of the six figures displayed at the bottom of the screen constituted the correct match for the moving shape. There were 120 trials and each one of the six shapes was the correct answer twenty times.

The results for this experiment are shown in figure 7.8b. The control subjects had near-perfect performance with approximately 95 percent correct responses. The patient O.S. scored in the normal range, while A.F.'s and M.S.'s scores of 16.7 percent correct responses were at chance. C.D scored above chance at 40 percent, but still, her results were significantly below those of the controls.

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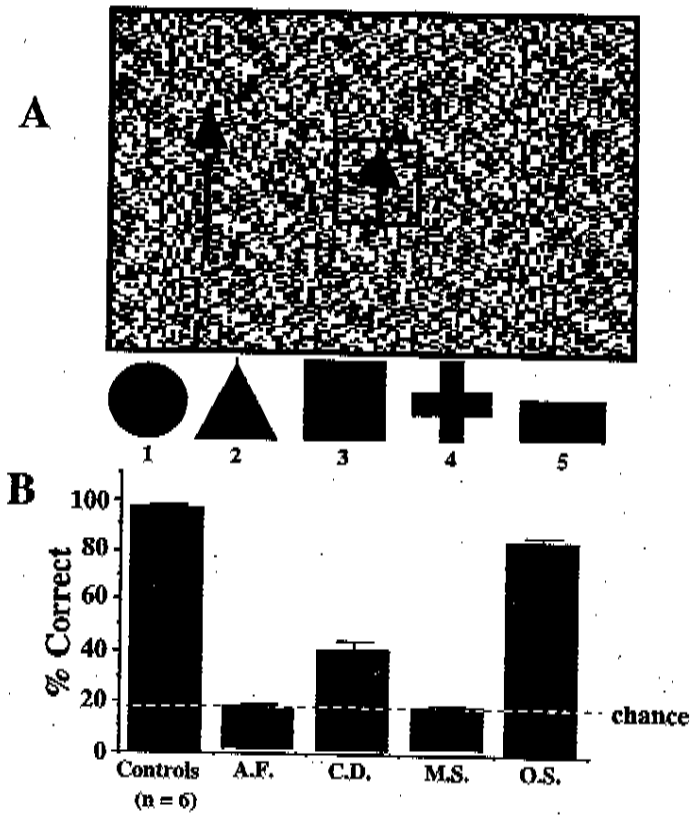


Figure 7.8 Two-dimensional form-from-speed differences. (A) Illustration of the stimulus. The random-dot pattern characteristics are the same as those in figure 7.5A. The background scrolls vertically and a central patch of contiguous dots subtending 2° × 2° moves in the same direction as the background with different speed. The shape of the central patch is randomly assigned to one of the five shapes illustrated on the bottom of the display. (B) Responses of control subjects and the patients. The bar graph plots percentage of correct responses of the total number of trials for A.F., C.D., M.S., and O.S., and the normal controls together with the standard deviation for the normal group and the standard errors for patients.

Experiment 5: Local Speed Discrimination

In this experiment, the stimuli consisted of two sparse dynamic random-dot cinematograms each comprising twenty dots. The cinematograms were displayed in two rectangular apertures arranged one above the other, each subtending an area of 4 × 2.5 degrees (figure 7.9a). The distance between the centers of the apertures was 2.75 degrees. In any single trial, each dot took a two-dimensional random walk of constant step size, which was determined by the speed. The direction in which any dot moved was independent of its previous direction and also of the displacements of the other dots. The speeds of the dots was uniform and was assigned independently to each aperture. A base speed of 3°/sec was always compared to five other speeds,

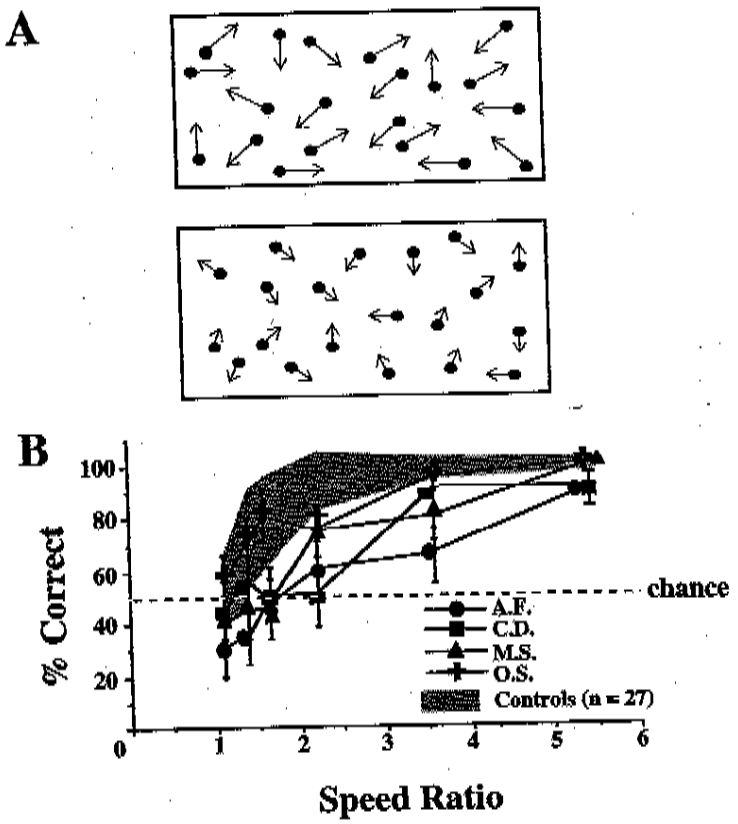


Figure 7.9 Local speed discrimination. (A) Illustration of the stimulus. The display consisted of two sparse random-dot fields each displayed in a rectangular aperture subtending 4° × 2.5°. Within each aperture the dots, plotted here as vectors, move in randomly distributed directions with constant speed. The observer's task is to decide in which of the two apertures the dots move faster. (B) Responses of control subjects and the patients. Results for A.F., C.D., M.S., and O.S. and twenty-six normal controls. The graph plots the percentage of correct answers as a function of the speed ratios between the two apertures. The data for the normal control group is presented as a shaded area representing mean ± one standard deviation. The patients data present the mean and the standard error.

giving speed ratios of 1.1, 1.47, 2.2, 3.6, and 5.5. The assignment of the highest speed to the top or bottom aperture was pseudorandomly selected. Each frame was on for 60 milliseconds with no interframe interval. A wrap-around scheme was used, in which dots displaced beyond the boundary of the aperture in the next frame reappeared on the opposite side.

In a two-alternatives, forced-choice discrimination task, observers were asked to determine which of the two apertures contained the faster moving dots.

In comparison to the control group, whose scores were almost perfect for the 1.47 speed ratio, A.F. was severely impaired on this speed discrimination

task. He failed to discriminate reliably speeds even at a ratio of 5.5 and performed at near-chance at ratios for which normal observers were performing better than 90 percent correct. Similarly, M.S. and C.D. were also severely impaired on this task, although C.D.'s performance at the ratios of 3.6 and 5.5 was close to the worst of the normal subjects. At ratios smaller than 3.6, M.S. and C.D. were very impaired. In contrast, O.S. performed in the normal range for all the speed ratios tested.

Experiment 6: Motion Coherence

In the final experiment, adapted from Newsome and Paré (1988), the stimuli were dynamic random-dot cinematograms with a correlated motion signal of variable strength embedded in motion noise. The strength of the motion signal, that is, the percentage of the dots moving in the same, predetermined direction, varied from 0 percent to 100 percent. For motion strengths less than 100 percent, the dots carrying the motion signal were embedded in a field of dots moving in random directions. At 0 percent, there was no motion signal (figure 7.10a, left), and at 100 percent, (figure 7.10a, right), all the dots moved in the same direction. In most of the trials, the subjects viewed a stimulus that was intermediate between the 0 and the 100 percent correlation conditions. Figure 7.10a, middle, shows a stimulus with 50 percent correlation.

The stimulus consisted of a dynamic random-dot display presented in a 10 × 10-degree aperture situated at 2 degrees left or right of a fixation mark. The subjects were instructed to maintain fixation for the entire testing period. The dynamic random-dot field consisted of one hounders dots.

The algorithm by which the dots were generated was similar to that of Newsome and Paré (1988). All the dots in the aperture had the same probability to be correlated with a dot in the next frame such that the displacements between the correlated dots was determined by the global motion. Thus, for example, if the probability was chosen to be 0.1, then the probability that a dot would continue on the same path for three consecutive frames was 0.001. Therefore, it is unlikely that the perceiver could follow a single dot or a local cluster of dots over several frames. Rather, the impression of coherent movement had to be derived from a global computation, which integrated the local motion measurements. The size of the step of the dots was held constant at 9 arcmin and thus, similarly to the previous experiments, this step is in the range of the values reported to fall within the spatial limits that characterize the short-range motion mechanism at the same retinal eccentricity (Baker and Braddick, 1982). Also as before, a conventional wraparound scheme was used. The speed of motion was roughly 3 degrees per second. The aim of this task was to determine the threshold of motion correlation for which a subject could reliably discriminate the direction of motion.

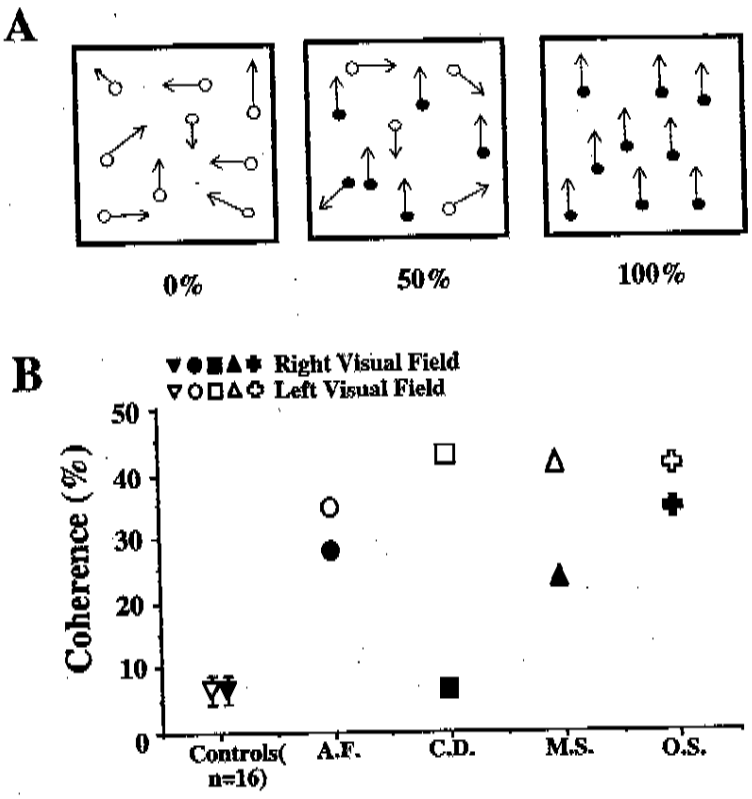
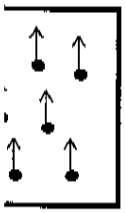


Figure 7.10 Motion coherence. (A) A schematic representation of the dynamic random-dot stimuli employed. Each stimulus presented dots in rapid succession and each dot survived for a brief period of time before being replaced. In the 0 percent correlation case, on the left, the replacement dots were plotted at random locations within the aperture so that the dot field appeared as twinkling visual noise without motion in any single direction. In the 100 percent correlation case, on the right, each dot was replaced by a partner with a constant offset in space and time, so that the dot field appeared to move in a single coherent direction. Intermediate states, such as that for 50 percent correlation displayed in the middle, a prespecified percentage of the dots carried the correlated motion signal while the remaining dots provided a dynamic masking noise. The stimulus is presented 2° to the left or to the right of a fixation mark. A four-alternative, forced-choice procedure was used to determine the threshold correlation for which observers could successfully discriminate the direction of motion. (B) The scatter graph plots the threshold correlation for sixteen normal controls and the four patients. The thresholds were determined by a staircase procedure as the mean of the last nine reversals. The open symbols represent thresholds for the right fixation mark, and the black-filled symbols represent thresholds for the left fixation mark. The dotted line represents the mean of percent correlation required by the sixteen normal controls. The thresholds for detecting the direction of motion for A.F., M.S., and O.S. were several standard deviations above the normals' threshold. The results of C.D. show that she was normal for the stimulus presentation in the left visual; her left visual field had very little residual vision, which explains the high threshold in this field.



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d.

Motion threshold was obtained in a forced-choice judgment of whether the perceived direction of motion was predominantly up, down, left, or right. The stimuli were displayed by an interactive staircase procedure driven by the subject's responses and controlled by computer. The staircase procedure went from easy to hard, such that after two consecutive correct answers the percent of correlated dots was reduced by one-eighth of a log unit of percentage of motion coherence. The percentage of correlated dots was increased after one incorrect answer. The test terminated after fifteen reversals (minima or maxima). The motion threshold was the average percentage coherence of the last nine reversals.

Figure 7.10b shows that the mean of the motion coherence threshold of the normal subjects (n = 16) was 6.5 percent for left fixation and 6.9 percent for right fixation. The thresholds of motion coherence obtained by the human observers in the Newsome and Paré task were roughly 2 percent. This may be accounted for by slight differences in the display characteristics and the fact that their subjects were trained observers, while the normal controls in this study were all naive observers. Also dot density in their task was roughly five times higher than in our display (1.7 dots/deg^2 square compared with 0.3 dot/deg^2). In addition, their subjects were experienced with psychophysical testing and received extensive training on the task. Our data (unpublished observation) also suggest the dependency of the threshold on training and psychophysical experience of the observer. The patients A.F., M.S., and O.S. were significantly impaired in this task in both the right and left visual fields. However, none of the four patients was impaired on a version of the motion coherence task in which the noise was static. Identical to the normals, their threshold was 1 percent, and a single dot moving was sufficient to detect motion and direction of motion. In contrast with the other three patients, C.D.'s performance was normal when the stimulus was presented in the intact visual field, but she could not do the task when the stimulus was presented in the blind visual field (this is not surprising since she could not do any task in the blind field). The elevated thresholds on the motion coherence task obtained by A.F., M.S., and O.S. suggest that they cannot compute global motion fields.

DISCUSSION

Computation of Visual Motion

In summary, the four patients studied here had different types of motion-related deficits. All patients were able to discriminate form-from-translational-motion. However, O.S. and A.F. were impaired on form-from-twinkling-motion, which brings further support to the hypothesis that Fourier and non-Fourier motion are mediated by distinct pathways. The patient O.S. performed well on the detection of motion inhomogeneities (figure 7.6),

localization of discontinuities (figure 7.7), two-dimensional form-from-speed-differences (figure 7.8), and local speed discrimination (figure 7.9) tasks. However, he was severely impaired on the motion coherence (figure 7.10). Conversely, C.D.'s performance was normal on this task (in the normal visual field) but not on the localization of discontinuities task (even when the notch was in the normal field). The patient M.S. essentially failed on all four tasks (except on the two-dimensional form-from-motion), and A.F. was severely impaired on speed discrimination and on motion coherence. Presumably, the differences between the patients reflected differences in the brain lesions caused by the patients' infarcts.

Were these patients impaired in their basic motion measurements, that is, could they measure direction and speed of motion? From the localization of discontinuities task, it seems clear that A.F. and O.S. had essentially normal directional discrimination. However, it appears that directional discrimination of M.S. and C.D. was impaired. However, although they failed on this task, they succeeded in a simpler directional task (figure 7.6). An explanation for the difference in performance in these directional tasks is that these two patients had normal directional discrimination, but could not localize motion discontinuities well, even within the range of their spatial localization abilities. Thus, although they were able to detect discontinuity defined by opposite directions of motion (figure 7.6B) they could not use this information to localize discontinuity (figure 7.7B).

The results of the speed discrimination task were more difficult to interpret. To discriminate speed one could use temporal discrimination; faster dots would remain for less time in the receptive fields. While temporal methods seem plausible in the local-speed task in which the dots' lifetime is short, we argue that this may not be the whole story. Speed signals are certainly available in the two-dimensional form-from-speed-differences task. In this task, dots live sufficiently long to allow precise speed measurement (McKee and Welch, 1985). Hence, it appears that A.F. and M.S. could not make basic speed and temporal discriminations. In contrast, O.S. and, to a lesser extent, C.D. seemed to have normal speed and temporal frequency mechanisms. Importantly, the correlation between the patients' performance in the two speed tasks suggests that temporal frequency speed discrimination processes are tightly coupled in the visual system (see also Pasternak, Horn, and Maunsell, 1989).

Another important question concerns how direction and speed of motion signals mediate the localization of discontinuities. There is evidence that comparisons between the results of absolute motion measurements made in neighboring regions of the visual field underlie this localization (Baker and Braddick, 1982; van Doorn and Koenderink, 1982, 1983). It has been suggested that these comparisons are made between full velocity signals (Nakayama and Loomis, 1974; Clocksin, 1980). However, our data do not support this suggestion, since A.F., who was severely impaired on speed, performed well on the localization of discontinuities task. It seems, therefore, more plausible

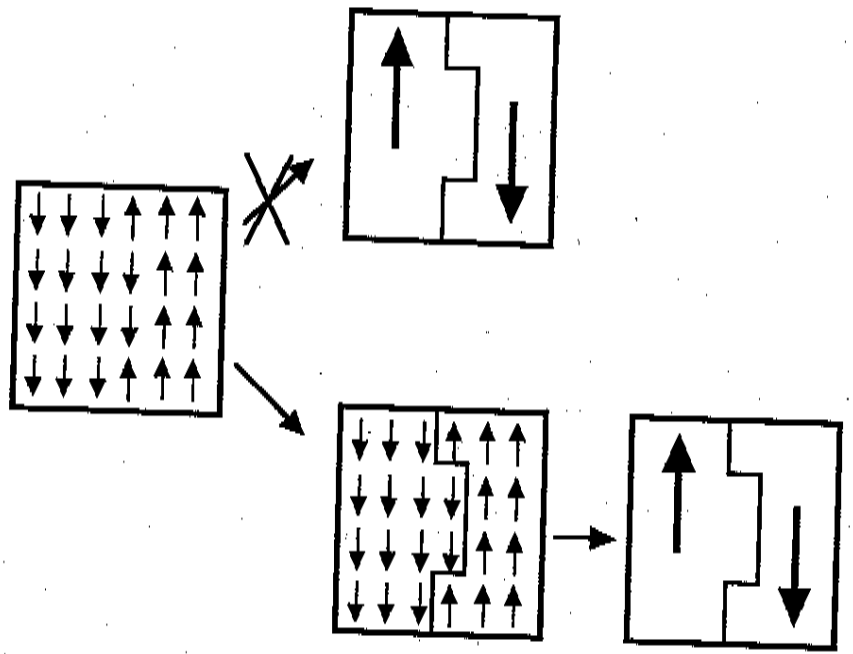

Figure 7.11 Two models of motion coherence. (A) On top, the Markov random field theory and line processor postulates that motion coherence and discontinuity are obtained in parallel. This is not supported by our data. (B) Our data suggest an alternate possibility: that the computation of boundary precedes the computation of coherence.

that A.F. only used directional measurements to localize discontinuities and that, perhaps, he disregarded speed information. But this does not imply that subjects discard speed or temporal information when they are available. On the contrary, the performance of normal subjects and of O.S. on the two-dimensional form-from-speed-differences task and on the localization of discontinuities at 0-degree angle-difference, suggests that discontinuities can be obtained from speed or temporal frequency signals alone. Hence, we conclude that direction-of-motion, speed, and temporal frequency discriminations can independently contribute to the computation of discontinuities.

Our data also address the issue of whether the computations underlying discontinuity localization and motion coherence occur simultaneously in the brain. These possibilities are suggested by theories based on Markov random fields and line processors (Koch et al., 1989) as shown in figure 7.11A. Roughly, these theories postulate the existence of two sets of cells. The first set, which we call the Markov set, tries to compute a coherent-motion field by minimizing differences in motion signal between neighboring cells via their synaptic circuitry. Simultaneously, the other set, which we call the line-processor set, measures whether the signal difference between neighboring cells in the Markov set is larger than a given threshold. If so, the line-processor set sends inhibitory signals to interrupt flow of information between the dissenting cells in the Markov set. Such a mechanism would predict that

if the computation of coherence is impaired, then so is the computation of discontinuity. In this case, the Markov set would be damaged and thus would not provide sufficient information for the line-processor set to work. Our data do not support this simultaneous-damage prediction, as C.D. performed well on the coherence task, but failed in the localization of discontinuities task. Further evidence against a simultaneous computation of discontinuities and coherence comes from A.F. and O.S.'s data. They both performed well on the localization of discontinuities task but were impaired in the coherence task. Thus, we conclude that discontinuity localization and motion coherence computation do not occur simultaneously in the visual pathway. We have shown this dichotomy between discontinuity computation and perception of motion coherence in another study (Vaina, Grzywacz, and Kikinis, 1994) of two patients with unilateral brain lesions (cases F.D. and A.M.G.). From a computational perspective, it seems desirable to account for the data by postulating that the computations of discontinuity localization and motion coherence are hierarchically organized, rather than occurring simultaneously (figure 7.11B). We suggest that information about discontinuity localization provides boundary conditions for the spatial integration that occurs in the computation of motion coherence. However, discontinuity information is not necessary for coherence. We suggest that computing coherence entails the integration of basic local motion measurements (directional, temporal, and speed signals). Thus, only local motion information is a sufficient input to computing coherence. We assume that the higher stages of motion processing have access to both coherence and discontinuity stages. According to this hypothesis, it is possible that different lesions may cause independent impairments in discontinuity localization and motion coherence.

To conclude, we would like to discuss briefly the performance of M.S. on the various motion tasks. Her right-hemisphere lesion is relatively small and cortical, and is in the position of the presumed human homologue of MT. (Her left-hemisphere lesion is mainly subcortical.) This patient is the most motion impaired among the patients reported here. The only task M.S. could perform reasonably well was a simple directional task (figure 7.5) in both the Fourier and non-Fourier (twinkling) condition. She had a curious performance in the localization of discontinuities task. She performed poorly at small and large directional differences, but seemed to be better at intermediate differences (45 degrees) possibly because she could somehow use the high-temporal frequency information available at intermediate directional differences. When dots travel diagonally relative to the boundary, some of them appear and disappear more quickly inside the notch than when they travel parallel or perpendicular to it.

Anatomical Implications

The delineation of the visual properties of specific areas of the extrastriate cortex of monkeys has generated a good deal of work in humans, which has

demonstrated submodality-specific deficits after focal brain lesions. Selective color discrimination (Damasio et al., 1980; Victor et al., 1989; Vaina et al., 1989), motion measurement (Holmes, 1918; Zihl et al., 1983; Hess, Baker, and Zihl, 1989; Vaina, 1988, 1989; Vaina et al., 1989, 1990a; Vaina, 1994; Baker, Hess, and Zihl, 1991), or face recognition impairments (Vaina et al., 1989) have been reported. Several studies based on anatomical (Horton and Hedley-White, 1984; Burkhalter and Bernardo, 1988) and molecular techniques (Hockfield, Tootel, and Zaremba, 1990) have shown that the organization and the pattern of connectivity of human cortex are similar to those of the macaque. Together with clinical and psychophysical studies in humans these studies demonstrate the existence of parallel processing streams in the human visual system. There is increasing neurological evidence (Vaina, 1989; Vaina et al., 1989, 1990, 1994) that a specialized stream of processing devoted to the analysis of visual motion exists in the human brain as in the monkey. Previous studies of motion deficits in patients with focal brain lesions (Holmes, 1918; Zihl, von Cramon, and Mai, 1983; Hess, Baker, and Zihl, 1989; Vaina, 1988, 1989; Vaina et. al, 1989, 1990a, 1990b) have shown that patients with lesions involving the occipital-parietal regions have selective motion deficits, while their ability to perceive form and color remains intact.

The area of the macaque cortex in which specialization of visual motion processing has been most clearly demonstrated is the middle temporal area (MT). It is believed that this area "concentrates and refines motion processing that is used for motion-dependent functions" (Wurtz et al., 1990). Recently several laboratories, including ours, became interested in finding a human homologue of the macaque MT area. Studies of changes in cerebral blood flow as monitored with positron emission tomography (PET) in normal human subjects observing low-contrast moving stimuli and fast flicker (Miezin et al., 1987), and dynamic random-dot patterns (Lueck et al., 1989; Zeki et al., 1991) and fMRI studies of expanding and contracting rings (Tootell et al., 1995) showed significantly increased activity in the region of the fundus of the occipital-temporal-parietal fossa (the area PTOF of Polyak, 1957, figure 271) situated near the intersection of the areas 19 and 37 (Zeki, 1990). These studies suggest that this region may correspond to the human MT. In a study of the cortical distribution of the pattern of myelination of the visual callosal afferents of the occipital lobes in the human brain, Clarke and Miklossy (1990) proposed a functional subdivision in areas 18 and 19 analogous to that of macaque visual areas. They suggested that, similarly to the macaque MT area, the putative homologue of MT in humans is also heavily myelinated, rich in callosal input, and located in the lateral occipital gyri, in area 19. This location corresponds to area 16 of Flechsig (Flechsig, 1920) and to Polyak's PTOF, and it was suggested that it might correspond to the human homologue of MT (Allman, 1977; Thurston et al., 1988; Zeki, 1991).

The above studies concur that the human homologue of the macaque area MT lies near the junction of the occipital, parietal, and temporal lobes. We

suggest that this region was disrupted by the lesions of M.S., A.F., and O.S., but it was spared in C.D. The patients A.F. and O.S. had large subcortical lesions. Figure 7.1 shows that A.F.'s lesion involved bilaterally the junction of the occipital and temporal horns with the bodies of the lateral ventricles (trigones of the lateral ventricles). The lesion in the right hemisphere is larger, and it extends into the medial and lateral portions of the temporal-occipital gyri and in the posterior parietal lobe. As discussed in detail in Vaina et al. (1990b,c), A.F.'s subcortical lesion probably undercut the circuitry underlying the junction between the occipital-parietal and temporal areas. The lesion of A.F. did not have any further cortical involvement. The lesion of O.S. involved bilaterally portions of the primary visual cortex and extended to the medial portions of the occipital horns of the lateral ventricles, and slightly into the posterior temporal lobes. The lesions of C.D. and M.S. were mostly cortical. As shown in figure 7.3, M.S.'s lesion involves the tip of the occipital poles and area 18 bilaterally. In the right hemisphere, the lesion extends forward to include the position of the junction of areas 19, 37, and 39, and the posterior parietal lobe. In the left hemisphere, the lesion is mostly subcortical extending from the occipital pole to the posterior temporal and parietal regions, and along the occipital horn of the lateral ventricle. The lesions of C.D. (figure 7.2) involve areas 18 and part of area 19 bilaterally, and part of area 17 in the right hemisphere. In the right hemisphere, the lesion also involves the junction of the inferior portion of the occipital lobe, and the middle and upper portions of the inferior temporal gyri. The lesion also involves the posterior portion of the parietal lobe. It is likely, however, that in both hemispheres, the junction of areas 19, 37, and 39 has been spared.

The patients A.F., O.S., and M.S, but not C.D., were impaired on the motion coherence task. Because the lesions in these three patients, but not in C.D., appear to involve the human homologue of MT, this suggests that in humans, MT may also be necessary for resolving ambiguity in a motion signal in order to extract the net direction of motion. (Newsome and Paré [1988] originally reported that monkeys with ibotenic-acid lesions to MT have elevated thresholds for discriminating direction of motion in a field of random noise.) The putative involvement of MT in the lesions of A.F., O.S., and M.S., but not of C.D., is consistent with the impairment of these three patients in the form-from-twinkling task. Recent data (Pasternak, Horn, and Maunsell, 1989) show that neurons in the cat's suprasylvian area, believed to correspond to the macaque's MT, respond to temporal frequencies higher than frequencies eliciting responses in the primary visual cortex. Thus, if a correspondence between MT and the cat's suprasylvian area exists, an MT lesion might cause a deficit in the detection of fast, transient visual events, necessary for solving the form-from-twinkling task.

The patients C.D. and M.S. were severely impaired on the perception of discontinuities from direction and speed. Since both A.F. and O.S. performed well on the discrimination of discontinuities from the difference of direction

of motion, we suggest that perhaps the area 18 involved in both M.S.'s and C.D.'s lesions is involved in the mediation of this computation. This is consistent with the finding that a large percentage (38 percent) of cells in the monkey's area V2 (area 18) have motion-antagonistic, center-surround organization (Lagae et al., 1988). Directionally selective cells keep their selectivity when a background stimulus moves opposite to their preferred direction. However, when the background moves in the preferred direction, the cells' response is suppressed.

Assuming that O.S.'s subcortical lesion disconnected MT (as illustrated in figure 7.4), his good performance on the tasks of extracting discontinuities from relative motion and on the speed task suggests that MT is not necessary for these tasks. (His ability to extract discontinuities is not surprising, since area 18 appeared to have been spared in his lesion.) However, there are alternative explanations for his good performance on the speed tasks: First, his lesion occurred several years prior to our examinations and it is possible that he might have recovered the ability to measure speed. Second, it is also possible that MT might not be totally disconnected but that it receives reduced input. In support of this explanation, his subcortical lesions were deep and might have spared some of the input to MT. Furthermore, since the primary visual cortex is involved bilaterally in O.S.'s lesion, it is possible that its remaining intact part and the intact portion of area 18 might contribute some information to MT, but this information is insufficient to solve the global task of motion coherence. Third, it is possible that O.S.'s intact posterior parietal region may mediate the speed tasks. Previous studies (Vaina, 1989; Vaina et al., 1990b, 1990c) and the results from C.D., A.F., and M.S. in this paper, show that patients with posterior parietal lesions are impaired in the speed tasks, while patients with lesions restricted to the posterior temporal lesions are not.

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