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Impairment of the perception of second order motion but not first order motion in a patient with unilateral focal brain damage

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SUMMARY

Unlike first order motion, which is based on spatiotemporal variations in luminance, second-order motion relies on spatiotemporal variation of attributes derived from luminance, such as contrast. Here we show that a patient with a small unilateral cortical lesion adjacent to human cortical area MT (V5) has an apparently permanent disorder in perceiving several forms of second-order but not first-order motion in his contralateral visual field. This result indicates that separate pathways for motion perception exist, either as divergent pathways from area MT or even from primary visual cortex, or as separate pathways from subcortical areas to extrastriate visual areas.

1. INTRODUCTION

Psychophysical studies of normal observers reveal two mechanisms by which we perceive visual motion. In first-order (Fourier) motion we detect real or apparent displacement of boundaries defined by luminance differences. In second-order (non-Fourier) motion we detect instead the displacement of boundaries where the amount of light on either side of the boundary is identical, but there is a difference in contrast produced by texture or flicker (Chubb & Sperling 1998; Cavanagh & Mather 1989; Wilson *et al.* 1992; Boulton & Baker 1993; Ledgeway & Smith 1994). Whereas first-order motion is conveyed by some shift of luminance distribution, in second-order displays there is no overall directional component of motion in the Fourier domain, and thus it has been argued that the visual system must perform nonlinear processing of the retinal illumination values, before performing the filtering operation which extracts motion. Salient features extracted through early vision, such as distinctive texture, colour, contour or flicker are potential cues for second-order motion.

Electrophysiological recordings from cells in the middle temporal area MT of monkeys (Albright 1992) and in extra-striate visual cortex of cats (Zhou & Baker 1993) have revealed cells that respond selectively to second-order motion, but any gross regional segregation of the two mechanisms remains controversial, despite clinical evidence that the two types of motion processing are dissociable (Plant & Nakayama 1993; Plant *et al.* 1993; Vaina *et al.* 1993).

Although selective disorders of the visual perception of movement caused by brain damage are rare, their

potential contribution to understanding how the visual cortex codes motion is as great as that of disorders of shape perception in revealing how shape is represented cortically. Motion blindness, i.e. almost total abolition of the perception of motion despite apparently normal perception of static visual displays has been reported, but the cortical lesion was large and extensively involved white matter (Zihl *et al.* 1991), making it impossible to attribute the disorder to destruction of any single cortical visual area. The first demonstration of an impairment that was purely unilateral and selective for second-order motion was made by Plant & Nakayama (1993) and Plant *et al.* (1993), who ingeniously used a cosine grating modulated in space by a cosine wave to provide a 'beat' stimulus whose direction of apparent motion was given only by the envelope of the waveform. They demonstrated enduring deficits in the contralateral visual hemifield of several patients with unilateral occipital lesions. The lesions were either large enough to include several putative extra-striate visual areas or, where small, involved white matter, again precluding any precise anatomical localization of the effective functional disruption. Patient FD is remarkable in having a confined and shallow lesion (see figure 1), probably sparing the putative human equivalent of the motion area of the macaque monkey (area MT) (Vaina *et al.* 1990; Watson *et al.* 1993; Tootell *et al.* 1995), but involving adjacent dorsolateral regions where, in monkeys, first and second-order motion coherence are also coded (Tanaka & Hikosaka 1986). Furthermore, his lesion barely encroaches on white matter, is also roughly 1/20th the volume of the lesion in the so-called motion blind patient (Zihl *et al.* 1991), and is unilateral, making it possible to compare motion perception in contralateral and ipsilateral visual fields of the same

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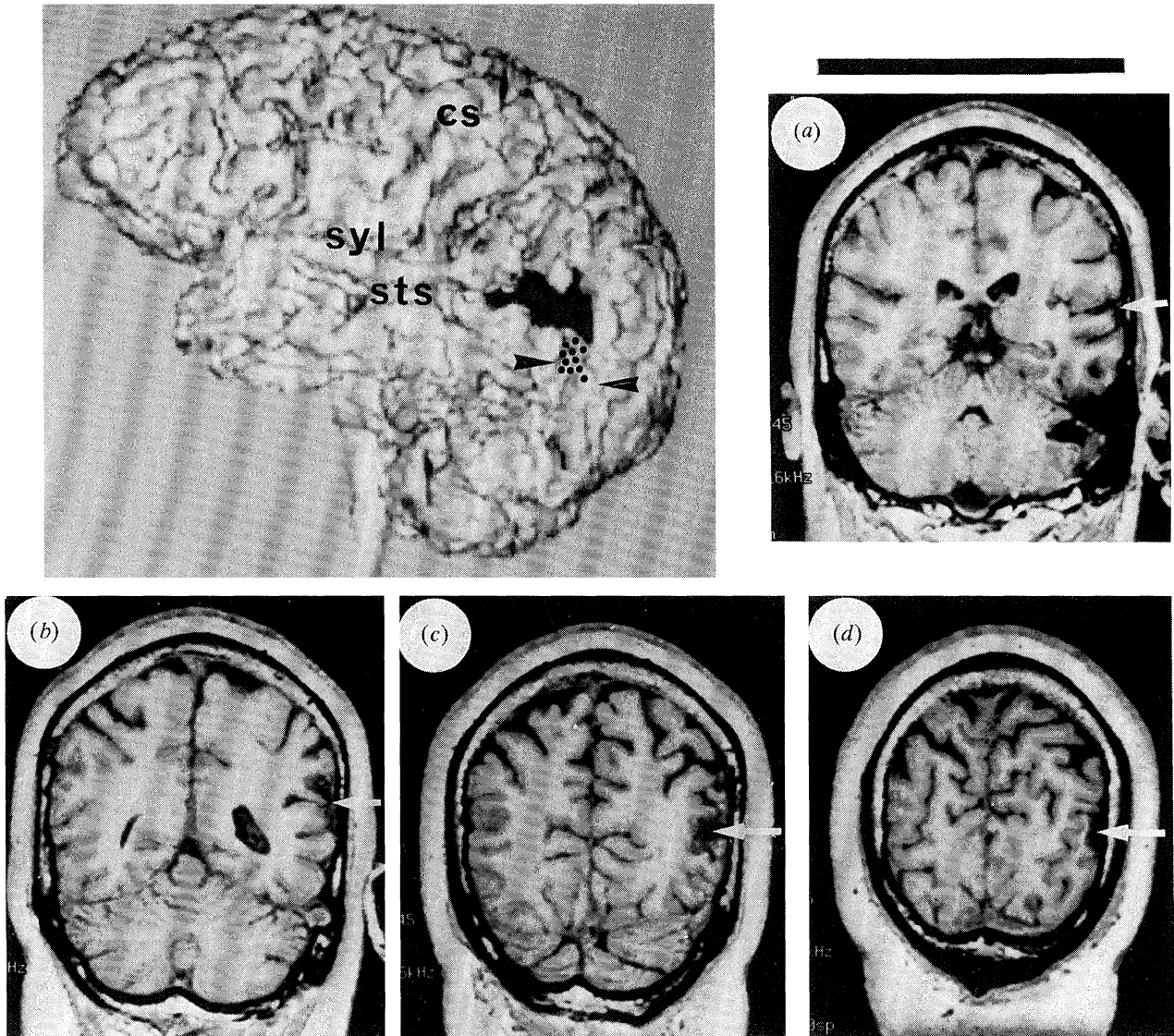


Figure 1. Lateral view of the left cerebral hemisphere of patient FD twenty months after his infarction and computer generated from his MR images. The superficial extent of his cortical lesion, black, was just dorsal to the dotted area that indicates the most likely position of the heavily myelinated region (Zilles & Schleicher 1993) and the region functionally activated by coherent global motion (Watson *et al.* 1993) believed to correspond to the 'motion area' MT or V5. Rostral and caudal arrowheads respectively indicate the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus. (a)–(d) Equispaced coronal MR images in the vertical plane of the figure through the lesion from rostral to caudal. The lesion, arrowed, is unusual in sparing underlying white matter and buried cortex. The plates are of high resolution T1-weighted MR gradient echo images, with a repetition rate (TR) of 35 ms, an echo time (TE) of 5 ms, and a flip angle of 45 deg. The acquisition was a 3DTF mode with a field of view of 24 cm² and a slice thickness of 1.5 mm. A total of 124 slices was generated and used to reconstruct the brain. Abbreviations: cs, central sulcus; sts, superior temporal sulcus; syl, Sylvian sulcus. Scale bar = approximately 13 cm for (a)–(d).

patient (Plant & Nakayama 1993; Vaina *et al.* 1994). We therefore examined his vision over a period of 30 months with respect to various examples of first and second-order motion.

2. SUBJECTS AND METHODS

(a) Subjects

Patient FD, a 41-year-old male right-handed college educated social worker, suffered a mild stroke with left hemisphere infarct in 1992 (figure 1). He had slight right-sided weakness from which he recovered in a few days, and mild anomia lasting a few weeks. He also complained of

feeling disturbed by visually cluttered moving scenes, and by auditory noise. Neuro-ophthalmological examination, including visual fields, was normal and his uncorrected acuity was 20/20 in each eye. When first tested within a few days and weeks of his stroke contrast sensitivity for detection of static or moving gratings and temporal frequency discrimination were normal. Discrimination of direction, speed or discontinuity of motion, and perception of 2-D and 3-D structure from motion were also normal, as were discrimination of orientation, spatial relations, form from luminance, stereopsis and colour. His scores on both the performance scale of the Wechsler Adult Intelligence Scale, Revised (WAIS-R) (PIQ = 97) and on visual memory for nonverbal material (83rd percentile) were average for his age and

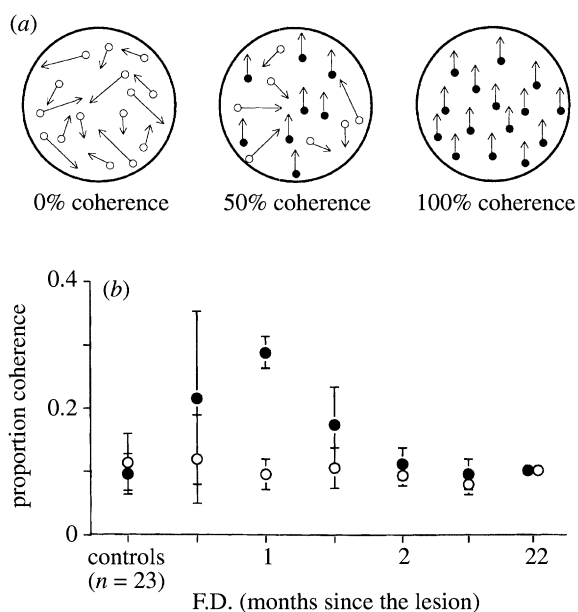


Figure 2. (a) Schematic examples of the first-order motion coherence stimulus (adapted from Newsome & Paré 1988). (b) Direction discrimination thresholds on the task shown in (a) for 23 normal control subjects (aged 22–44 years) and for patient FD at different time intervals after his infarction. (hollow circle) and (filled circle) respectively show thresholds for stimuli presented in the left and right visual field. Bars show ± 1 s.e. In this and other figures the absence of an error bar indicates that it was not possible to do more than one testing session.

education. On nonverbal measures of attention (adapted from Corbetta *et al.* 1991) he performed in the normal range for both selective and distributed attention to colour, form and speed.

Control subjects were normal observers, male and female, right-handed, and mostly in their twenties. Whenever there were clear age-related differences in performance within the control group, only the results from control subjects of similar age to FD were used. All subjects, including FD, gave informed consent before participating in the investigations.

(b) Tests of first-order and second-order motion

Stimuli were generated and data collected by a Macintosh Quadra computer and displayed on the Apple 13 inch high resolution RGB monitor. The image was refreshed every 66Hz and luminance output on the screen was calibrated for linearity using a luminance meter (Minolta LS110). The experiments were done in a darkened room in which the only ambient lighting was provided by the display screen. For all but one test (Gabor patches) subjects sat 60 cm from the screen and fixated a small black fixation mark at eye level and 2° to the left or right of the imaginary outer margin of the stimulus. The subject's spoken vocal responses were entered on the keyboard by the examiner. Each 1 s stimulus presentation involved 22 frames, each frame lasting 45 ms. Thresholds for discriminating direction of motion were measured by forced-choice methods and an adaptive staircase procedure that tracked 79% correct performance. After ten reversals the threshold was calculated as the mean of the final six reversals. A step size of 0.09 log units was used for the first reversal, 0.06 log units for the next reversal, and 0.03 log units for the remainder.

(a) First-order motion: high contrast motion coherence

The simplest first-order motion coherence displays (figure 2) were adapted from Newsome & Paré (1988). The stimuli were stochastic random dot cinematograms with a coherent motion direction signal of variable strength embedded in masking motion noise, presented in a circular aperture 10° in diameter and with a dot density of 2 dots deg^{-2} . The speed of the signal dots was 3 deg. s^{-1} . The dots were 2 arc. min in diameter and were of high contrast, but their low space-time density produced an average luminance of only 0.51 Cd m^{-2} against a background luminance of 0.24 Cd m^{-2} . At 100% coherence (figure 1, right), each dot was replaced by a dot with a constant offset in space and time. At 0% coherence, the replacement dots were plotted at random locations within the aperture so that the dot field had no perceptible coherent motion in any direction. In the intermediate state, exemplified here by 50% coherence, a specifiable proportion of dots carried the coherent motion signal while the remainder provided masking noise. During one trial, every dot had the same probability of being correlated with a signal dot in the next frame, such that the displacement between the correlated dots was determined by their global motion. The impression of movement had to be derived from a global computation, which spatially integrated local motion measurements. Using a forced four-choice procedure subjects had to report the direction of global motion: up, down, left, or right. Perceptually, the subjects did report global rather than local motion.

(b) Second-order motion: flickering bars

Direction discrimination of second-order motion was first assessed using the 'movement without correlation' display (Albright 1992) shown in figure 3a. The display was a dense array of static random dots (10×10 deg., mean luminance 28 Cd m^{-2}) within which a horizontal bar, in which some proportion of the dots flicker, appears to move up or down the display. It is the flicker that provides the signal, with no overall change in luminance or unique pattern of luminance within the bar. In each temporal frame (15 ms) spatially consecutive imaginary square-wave bars with spatial frequency of 0.2 cycles deg^{-1} and temporal drift frequency of 6 Hz (= c. 30 deg s^{-1}) were replaced by different uncorrelated random patterns of equal density and temporal frequency. The percept was a bar composed of flickering dots, drifting smoothly up or down, where the flickering was obtained by randomly inverting the contrast of a given proportion of dots in each frame within the bounds of the bar. The density of the flickering dots (50% and 20% in figure 3) was varied by an adaptive staircase method which controlled the salience of the bar. In a 2AFC task, the subjects had to discriminate the direction of vertical motion. The rapid drift rate made feature tracking impossible whether or not the subject maintained fixation.

(c) Second-order motion: Gabor patches

Second-order moving stimuli typically introduce substantial 'noise' in mechanisms sensitive to first-order motion and FD could be impaired on second-order motion because he is abnormally sensitive to and confused by noise, whether spatial or temporal, in the first-order system. To control for this possibility we tested him with a display (figure 3c) adapted from Green (1986), where the viewer must decide whether the two pairs of Gabor patches appear to 'rotate' in a clockwise or anticlockwise direction. This particular

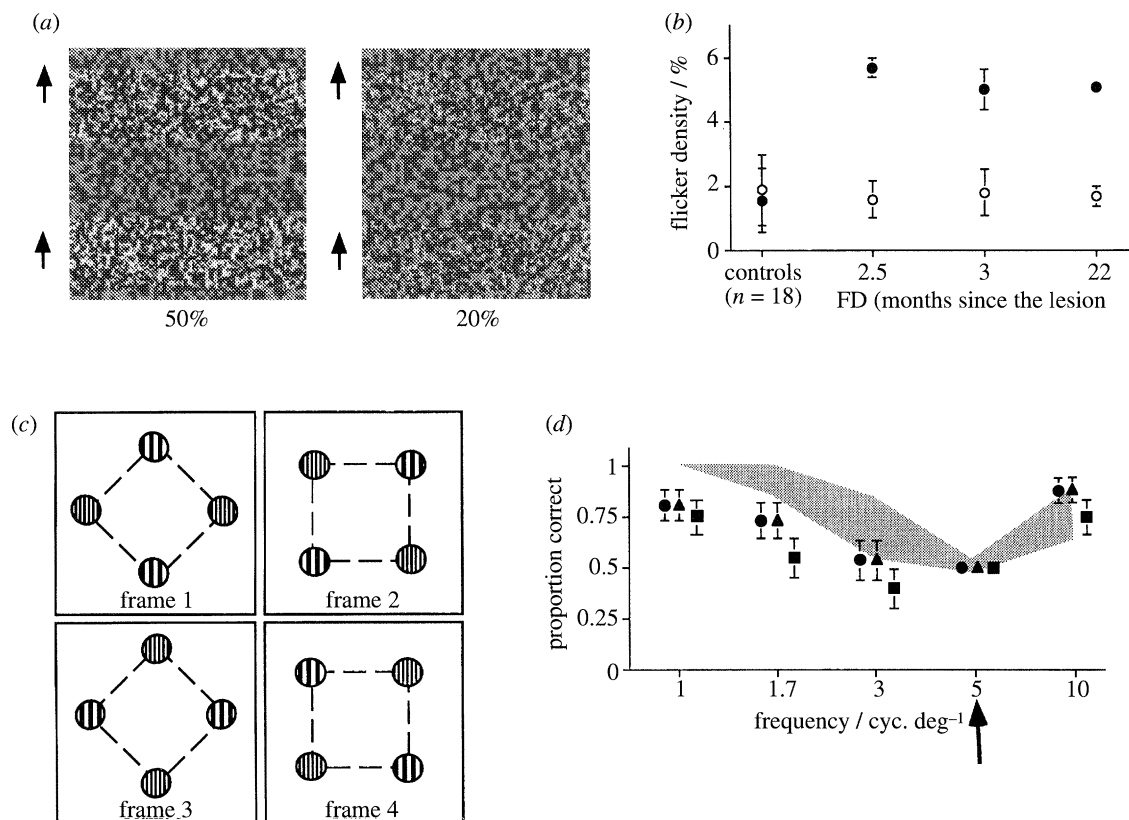


Figure 3. (a) Two single frames of the display used to generate second-order movement without coherence. The dots are static but the position of the bars within which some dots flicker shifts up or down. (b) The percentage of flicker needed to sustain reliable discrimination of direction of motion in the task illustrated in (a) is shown for 18 normal control subjects (aged 19–46) and for FD at various times after his infarction. Thresholds are shown for stimuli presented in the left (hollow circle) and right (filled circle) visual hemifields. (c) Schema for second-order motion using long-range conditions and Gabor-patches (adapted from Green 1986). (d) Per cent correct responses as a function of the spatial frequency values of the test Gabor pairs. The data from 16 normal controls (aged 27–48 years) are presented as a shaded area representing the mean ± 1 s.e. FD's results, mean and standard errors, are from three experimental sessions 0.5 months after the infarction (squares), after 2.5 months (triangles), after 22 months (circles). His performance on the two control tasks (see text) was within the range of the 95 percentile of the normal controls.

example of second-order motion is also called long-range motion (Braddick 1974). What must be detected is the change in position of Gabor patches, which are otherwise unvarying and should therefore not introduce 'noise' to first-order detectors. The viewer discerns movement from the translocation of textures. In each trial the display consists of two pairs of vertically oriented Gabor patches positioned orthogonally to each other and grouped around a cross-hair fixation point (figure 3). The Gabors of each pair have the same spatial frequency and during 'rotation' only the positions of Gabors are changed, not their orientations. One pair of Gabors, the standard, was held constant at 5 cycle deg^{-1} . The other pair, the test, could have one of five different central spatial frequencies: 1, 1.7, 3, 5 and 10 cycles deg^{-1} . The separation of like Gabors is 3.6° and for a 45° rotation each travels 1.4° . At 100% contrast each Gabor subtends 1.7° . As Gaussian modulation hides the edge of an object the perceived size is a function of the contrast of the Gabor and the contrast sensitivity of the observer. Mean luminance of the display was 24 Cd m^{-2} . Viewing distance was 125 cm and stimuli were displayed by the method of constant stimuli (24 trials per data point). In a 2AFC task subjects had to discriminate the direction of apparent rotation. Schema of frames used in each trial is shown in figure 3c. A total of eight frames (each visible for 75 ms) interleaved with seven inter-stimulus intervals of 45 ms each, were displayed in one of two sequences, corresponding to

clock-wise (presenting the frames in the order 1, 2, 3, 4) or counter-clock-wise rotation (order 1, 4, 3, 2). These display times and the inter stimulus interval were chosen because they produced the strongest impression of apparent rotation. To control for the possibility that apparent contrast of Gabors might influence apparent motion two prior control tasks were used. First, the subjects were shown all four Gabors and asked to adjust the contrast of each Gabor until they had the same apparent contrast. Second, to control for the possibility that subjects can not detect the difference in spatial frequency, a static task was used in which three Gabors have the same spatial frequency and the fourth is different. The subjects' task was to pick the odd one out and FD was unimpaired.

(d) *First and second-order motion at low luminance contrast*

With the kind of display shown in figure 2 any unimpaired performance on first-order global motion might be attributable to the high luminance contrast of the displays, because stimuli of high luminance contrast can contain both first- and second-order motion cues. We therefore compared performance, by using 2AFC, on the two forms of motion using displays in which possible contaminating effects of luminance contrast were eliminated. The displays in figure 4a,b are conceptually identical to those of figure 2 except that

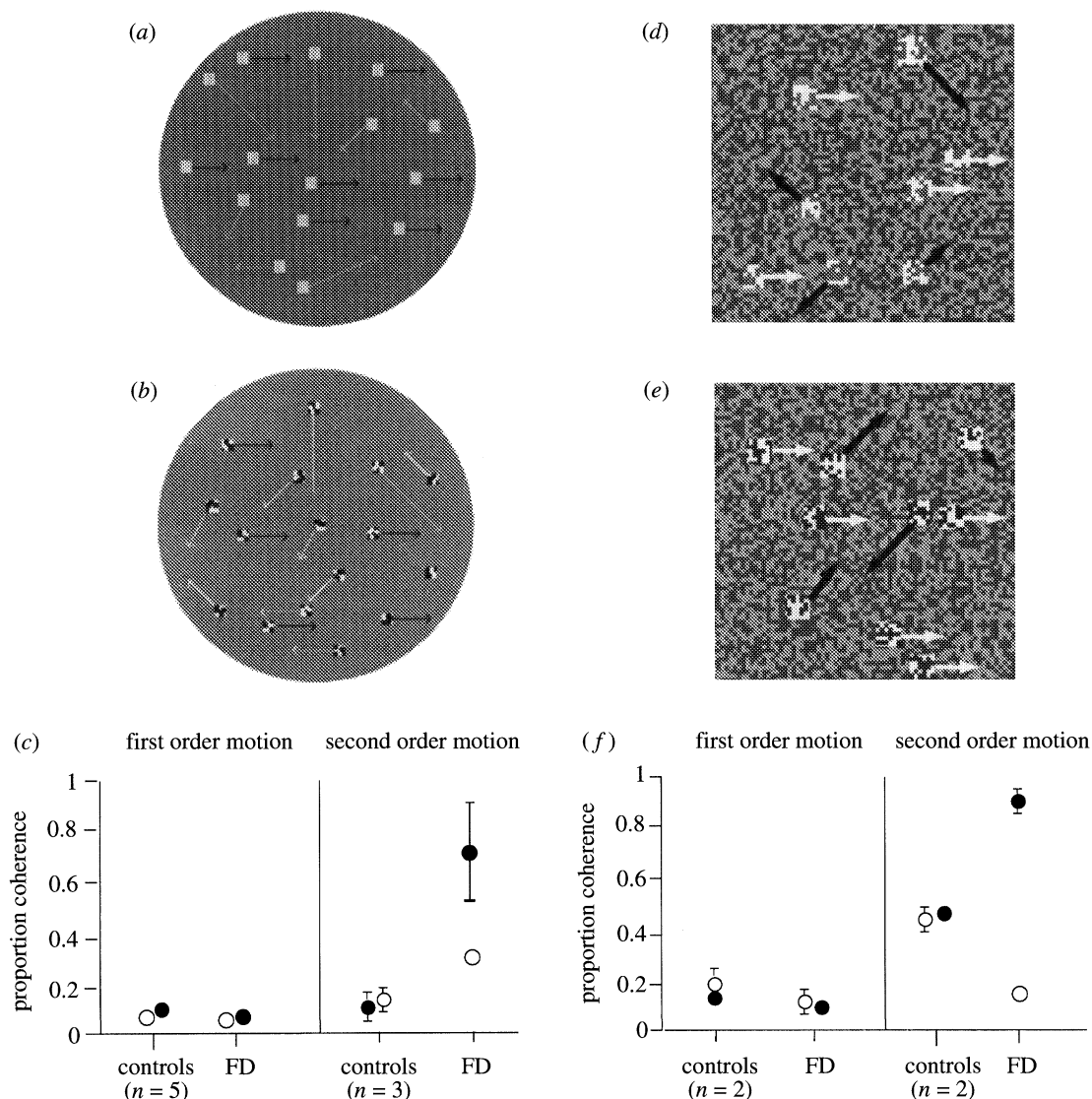


Figure 4. Displays using low contrast first-order motion coherence and high-contrast first- and second-order motion coherence. In the two pairs of experiments schematically portrayed in (a), (b), (d), and (e) the algorithm for generating global motion was identical to that of figure 2. The crucial changes were in terms of the difference between the moving items and the background in luminance but not contrast (the first-order tasks) or in contrast but not in luminance (the second-order tasks). (a) Schematic view of the low contrast, first-order motion coherence task, at 50% coherence. Stimulus display is 10° in diameter, and motion item density is $2 \text{ items (deg}^{-2})^{-1}$. Each item subtends 12×12 arcmin, and their speed is 3 deg s^{-1} (identical to experiment 1). The mean background luminance is 12.3 Cd m^{-2} and the luminance of the items was established by the control experiment described below. (The specific values used was 12.4 Cd m^{-2}). (b) The second-order motion coherence task at 50% coherence. The moving items consist of binary-noise texture of identical mean luminance to the background. The texture-noise defining the moving items is independent from frame-to-frame. Each moving item subtended 12 min^{-2} , and its texture resulted from its combination of bright and dark pixels. The background luminance was identical to that of the stimulus described in (a). (c) Threshold of coherence necessary to discriminate direction of motion for F.D. and for age matched controls. The data for FD were obtained 22 months after his infarction. Thresholds are shown for the left (hollow circles) and right (filled circles) visual hemifields. (d,e) Schematic view of the stimuli at 50% coherence in the final pair of first and second-order motion coherence tests. In these global motion experiments the background now consists of a field of randomly flickering binary noise of contrast 0.25 and in the low-contrast first-order version (d) the moving items (subtending 12 min^{-2}) differ from the background only in luminance, not in texture-contrast. In the second-order version (e) the moving items (again 12 min^{-2}) have the same mean luminance as the background, but a higher texture contrast. The speed of the moving items was 5 deg s^{-1} . As a control (not shown) to equate the salience of the first-order and second-order signal elements we used a simple static detection task for each type of signal element and accordingly adjusted its luminance (first-order version) or its contrast (second-order version) until the subject successfully detected them at 80% correct. (f) The coherence necessary for reliable discrimination of opposite directions of motion (left versus right) by FD and age matched normal controls in the left (hollow circles) or right (filled circles) visual hemifield. FD's data were obtained 30 months after his infarction.

in figure 4*a*, first-order coherent motion, the constant difference in luminance between the moving tokens (9.6 Cd m^{-2}) and the background (10.3 Cd m^{-2}) is now slight instead of prominent, and in figure 4*b* the tokens giving rise to second-order motion are micropatterns of binary noise textures whose mean luminance, although varying slightly from frame to frame, is on average identical to that of the surround but whose within-pattern contrast is much higher. The texture of the micropattern is independent from frame to frame. Although there is inevitably some first order motion energy in this stimulus, it is unsystematic with respect to correlated motion. All moving tokens subtended 12 arcmin.

(e) First and second-order motion with noisy backgrounds

As the spatial frequency content of the second-order motion displayed in figure 4*b* is broadband, any apparent selective impairment in the perception of second-order motion could arise from a susceptibility to the effects of masking. To test this we used 2AFC procedures to compare direction discrimination, with respect to first and second-order motion displays where both contained a noisy background of identical spatial frequency content and where the moving tokens were defined by a textured micropattern. In figure 4*d* the first-order movement was generated by elements whose mean contrast with the now flickering surround is provided by luminance but not texture contrast whereas in figure 4*e*, showing second-order motion, the contrast arises from texture differences but not (mean) luminance. As the micropatterns are randomly replaced from frame to frame, what moves in *d* and *e* is a patch of different mean luminance or different contrast respectively.

3. RESULTS

(a) First-order motion: high contrast motion coherence

For about a month after his stroke FD was impaired at discriminating the direction of coherent movement in simple dot displays made up of first-order motion (figure 2) when they were presented in his contralateral visual field (Vaina *et al.* 1994). This was the only first-order task on which he was ever impaired; his direction discrimination in the absence of noise, or with only a small percentage of noise introduced to prevent tracking eye movements, was normal. The impairment had disappeared within 2 months (figure 2), reminiscent of the recovery in monkeys on the same task after being given small ibotenate lesions in area MT (Newsome & Wurtz 1988), and remained unimpaired after 22 months. His perception of simple first-order motion and its contribution to computing motion coherence are evidently normal.

(b) Second-order motion: flickering bars

Figure 3*b* shows that for displays presented contralaterally to his lesion patient FD required about three times more flickering elements than normal to perceive the direction of second-order apparent movement.

(c) Second-order motion: Gabor patches

The effects of using a second-order motion display designed to minimize the introduction of any con-

taminating 'noise' into the first-order system is shown in figure 3*d*. Patient FD, tested from 2 weeks to 22 months after his stroke, was permanently impaired. Even though he was fixating the centre of the display, both hemispheres have to be intact for the normal perception of the illusion.

(d) First and second-order motion at low luminance contrast

It was to control for the possibility that second-order motion is impaired in FD because the individual moving tokens are less salient than in first-order motion that we did the procedure shown in figure 4. The first-order display contains moving micropatterns that differed from the surround in luminance but not contrast, whereas in the second-order display the micropatterns differed from the background in contrast but not in luminance. FD's performance was identical and normal in both visual hemifields for first-order motion (figure 4*c*), despite the faint contrast of the tokens, but was grossly impaired in his right hemifield for second-order motion, even though the individual tokens in the latter were more salient.

(e) First and second-order motion with noisy backgrounds

A similar result was obtained when using displays with a noisy background and textured micropatterns as the moving tokens to make the entire display broadband (figure 4*c*). FD performed normally in both visual hemifields with first-order motion but with second-order motion in his right visual hemifield he was so badly impaired that he required 90% coherence to see the motion. That he was actually better than control subjects in his normal hemifield probably reflects his more extensive practice. Across all tasks he was as good as or better than normal in this hemifield.

Finally, to control for the effects of noisy displays *per se* we tested his ability to see static fragmented letters and shapes embedded in a static random dot background, using a staircase procedure to vary the extent of the fragmentation. He was normal in both hemifields.

4. DISCUSSION

A total of three types of second-order motion tasks were used, all addressing direction discrimination. In the 'flickering bar' test, to extract direction the visual system is thought to perform a temporal frequency filtering followed by a rectification. In the experiment using rotating Gabor patches to create clockwise and anticlockwise direction, the visual system must first do a spatial frequency filtering of the stimulus and then a rectification. In the last two tests of motion coherence, a rectification operation on the stimulus will generate a first-order motion coherence stimulus. As FD was impaired on all four second-order motion tests, but not on first-order motion tests, including the motion coherence, it is possible that he cannot adequately perform the necessary rectification. A selective effect

on second-order motion was first described in several patients by Plant & Nakayama (1993) using contrast modulated gratings and by Vaina *et al.* (1993). The present results demonstrate that the dissociation occurs with a range of tasks involving motion coherence, that it includes global as well as local motion and that it can arise from a small, circumscribed and chiefly cortical lesion at the junction of the occipital, temporal and parietal lobes. Superficially (without knowing the psychometric function) FD's second-order impairment was least when using Gabor patches. This might reflect the possibility that there is a third motion sensitive mechanism (Lu & Sperling 1995) which receives input from both of the other lower level systems and whereby long range token matching is achieved without a simple rectifying nonlinearity.

It has been proposed (Wilson *et al.* 1992) that while first-order motion is registered in the primary visual cortex (V1), the detection of second-order motion requires further computations in extra-striate areas such as V2 and MT. Recent attempts to dissociate the two mechanisms, based on scalp recordings of slow cortical potentials, were not successful (Patzwahl *et al.* 1994), perhaps because, as in monkeys, there are several visual areas in the immediate vicinity of area MT, all registering first-order motion and some of which additionally compute second-order motion (O'Keefe 1993).

Could the cortical lesion in patient FD be the 'motion' area MT (V5) itself? The admittedly inconclusive evidence does not favour this view. At first we believed that FD's lesion was adjacent to the caudal tip of the Sylvian fissure. The computer generated surface rendering (see figure 1) shows instead that it straddles the caudal portion of the superior temporal sulcus and no experimental study known to us has placed human area MT (V5) quite so dorsally. Instead, based on myeloarchitecture (Zilles & Schleicher 1993) or the pattern of callosal connexions (Clarke & Miklossy 1990), area MT lies ventral to the caudal end of the superior temporal sulcus, just below FD's lesion. Functional neuroimaging designed to activate human area MT also places it ventral to this region (Watson *et al.* 1993; Tootell *et al.* 1995). In the most extensive study of its – somewhat variable – position in 12 subjects it lay near the real or imagined confluence of the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus, especially in the caudal bank of the former (Watson *et al.* 1993). However, functional neuroimaging studies of normal subjects have shown activations in the region of FD's lesion elicited by small 3° moving dot patterns (Dupont *et al.* 1994) or large field moving displays (Cheng *et al.* 1995). As there is abundant evidence for multiple extrastriate visual areas in macaque monkeys, in several of which the cells are specialized for detecting various forms of movement e.g. area MST just above area MT (for review see Maunsell & Newsome 1987), the precise localization of FD's lesion may seem merely academic. The reason it is not is that its more dorsal location supports suggestions that second-order motion might be computed, or further computed, after initial analysis in area MT, or even without involving area

MT. This could be resolved by studying patients with small lesions centered on area MT and by comparing the effects of removing area MT and the motion areas dorsal to it on first and second-order motion in monkeys. It would also be illuminating to do functional magnetic resonance imaging on patient FD, especially to see whether displays appropriate for revealing area MT reveal its preservation in the damaged hemisphere and/or its position in the undamaged hemisphere.

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