

Motion and shape perception in cerebral akinetopsia

Matthew Rizzo,¹ Mark Nawrot¹ and Josef Zihl²

¹*Division of Behavioral Neurology and Cognitive Neuroscience, Department of Neurology, The University of Iowa College of Medicine, Iowa City, USA and the* ²*Max Planck Institute Für Psychiatrie, München, Germany*

Correspondence to: Matthew Rizzo, MD, Division of Behavioral Neurology and Cognitive Neuroscience, Department of Neurology, The University of Iowa Hospitals and Clinics, Iowa City, IA 52242, USA

Summary

Motion cues serve many purposes in primate vision. Consequently, akinetopsia, a defect of movement perception due to cerebral lesions, would be expected to comprise a range of motion-related defects. To address this issue we explored further the perceptual profiles in akinetopsic subject L.M. who has motion perception deficits due to extensive bilateral lesions of the dorsolateral visual association cortex that spare primary visual cortex, area V1. We used several different experimental procedures. Using random-dot motion stimuli, we showed that L.M. can still perceive global coherent motion and discriminate motion direction, yet these abilities fail even at moderate levels of background noise. L.M. also viewed a two-frame apparent (phi) motion stimulus known

as a Ternus display. Her performance on this test suggests defective 'long-range' apparent motion mechanisms. These results are clearly in agreement with previous reports. Additional experiments showed that L.M. can still perceive 2-D shape and 3-D structure-from-motion (SFM). However, like motion direction discrimination, these abilities broke down at moderate levels of moving and stationary noise. Surprisingly, L.M. also had trouble perceiving 2-D shapes defined by non-motion signals including 'on' and 'off' transients, dynamic and static binocular disparity, and static texture cues. Our findings highlight the role of the visual association cortex in extracting salient information from noise.

Keywords: akinetopsia; area MT (V5); form-from-motion; motion perception; structure-from-motion; visual cortex.

Abbreviations: AFC = alternative forced choice; AM = apparent motion; BVRT = Benton Visual Retention Test; CFT = complex figure test; CS = contrast sensitivity; HVOT = Hooper Visual Organization Test; ISI = inter-stimulus interval; LCD = liquid crystal display; MT = mesial temporal; RDC = random-dot cinematograms; SFM = structure-from-motion

Introduction

Ten years ago, Zihl *et al.* (1983) reported the case of patient L.M., who had a severe disturbance of movement vision following damage to the posterior sectors of both hemispheres. L.M. showed a deficit for movement perception in several tasks. She could see movement in light targets moving horizontally or vertically below 10–14°/s, but with higher velocities she was uncertain whether targets moved or were stationary. In such conditions she reported the appearance of the target at successive positions with no movement in between. Similarly, she could follow with her eyes a target moving at 4°/s, but at 8°/s had saccadic pursuit. She could not track the trajectory of her own right index finger if it moved 'too fast'. L.M. underestimated the speed of targets moving at 12°/s and 24°/s, but not at 3°/s or 6°/s. She also had a defect of the phi mechanism, which normally allows

us to perceive apparent motion between successive static frames in an animation sequence, such as a Hollywood movie. Furthermore, L.M. had reduced perception of motion after-effects, and the spiral after-effect elicited no sense of motion-in-depth. Finally, she reported seeing changes in position but not movement-in-depth when a black cube lying on a table was moved toward and away from her.

The motion vision disturbance in L.M. was relatively selective: she had good visual acuity and no reported visual field defect for form or luminance. Thus, she could detect stationary light targets (0.3–320 cd/m²) presented binocularly in a Tübingen perimeter. Tactile and acoustic motion perception were reportedly normal. Similarly, thresholds for resolving the temporal flicker of a light presented at several locations in the fovea and peripheral fields, and the amplitudes

and latencies of visual evoked potentials generated in response to contrast reversing checkerboard stimuli were all normal. Static binocular stereoacuity and manual reaction times to visual targets were modestly impaired, yet there was no neglect of visual targets flashed simultaneously in both hemifields, and electro-oculography showed accurate localization of visual targets by saccadic eye movements. Moreover, the striking preservation of face and object recognition, reading, and colour vision distinguished L.M. from subjects with damage in ventromesial visual association cortices, located below the calcarine fissure in the occipital lobe and in adjacent inferotemporal regions. Zeki (1991) labelled L.M.'s deficit 'cerebral akinetopsia', mimicking the term 'cerebral achromatopsia', used to describe the human cortical colour processing defects.

The case of L.M. was important in spurring further research on a cortical substrate for motion perception. The lesions in this benchmark case (Zihl *et al.*, 1991) and in subsequent subjects with reported motion perception deficits (e.g. Thurston *et al.*, 1988; Vaina, 1989; Vaina *et al.*, 1990; Beckers and Hömberg, 1992; Morrow and Sharpe, 1993; Plant and Nakayama, 1993; Plant *et al.*, 1993) include structures in an occipito-temporo-parietal and a parieto-occipital location. These dorsolateral visual association cortices coincide with loci of activation identified in PET studies in normal subjects viewing moving stimuli (Corbetta *et al.*, 1991; Watson *et al.*, 1993). These cortical areas include Brodmann's (1909) classical cytoarchitectonic area 19 and adjacent area 37. From criteria of myelogenesis (Flechsig, 1901), myeloarchitecture, and callosal connections, part of these areas may resemble the monkey mesial temporal (MT) area (Allman, 1977; Clarke and Miklossy, 1990), also known as V5 (Dubner and Zeki, 1971; Zeki, 1974). Area MT (V5) contains neurons that are sensitive to stimulus direction, speed, orientation and binocular disparity (Maunsell and Van Essen, 1983 *a, b*), that are active during perceptual decisions on these properties (Salzman and Newsome, 1994), and that probably contribute to motion direction discrimination (Newsome and Paré, 1988), and even shape-from-motion perception (Schiller, 1993).

While the anatomical locus and extent of brain lesions in patients with defective motion vision is an active research topic, the range of perceptual deficits and residual abilities in affected patients remain under-explored. Moreover, the main indices used to diagnose defective motion processing have varied widely. For example, some investigators have used smooth pursuit eye movements alone to infer a motion vision defect while performing no afferent testing of motion (Thurston *et al.*, 1988). Furthermore, motion plays many roles (Nakayama, 1985), and consequently cerebral akinetopsia should comprise a range of motion-related defects. Profiling these defects would be expected to provide more insights on the nature of cerebral akinetopsia and on the role of a human cortical network for motion perception. To date, L.M. is perhaps the akinetopsic subject whose visual deficits have been studied in the greatest detail (Zihl *et al.*, 1983; McLeod *et al.*, 1989; Hess *et al.*, 1989; Baker *et al.*, 1991). The

experiments of Hess *et al.* (1989) and Baker *et al.* (1991) are of key importance and raised several issues that motivated the current study.

Motion discrimination

Hess *et al.* (1989) noted that normal motion vision requires first that spatial and temporal filters be intact, and second that outputs of these filters be available for comparison. They determined that L.M.'s contrast sensitivity (CS) for simple detection of sine wave gratings showed only small loss even for moving gratings, but CS dependent on discrimination of motion showed a large loss. Also, spatial frequency and CS discrimination were much better than temporal frequency or velocity discrimination for the same moving and stationary stimuli. The findings suggested that L.M. has a motion performance deficit affecting judgment of stimulus and motion attributes, not the detection of motion *per se*.

To determine whether L.M.'s residual performance was due to inferences from non-motion cues, such as counting the passing bars per unit time in drifting gratings, Hess *et al.* (1989) used double flash random-dot cinematograms (RDC). These stimuli depicted two sequential arrays ('frames') of spatially random dots, the second being identical to the first but displaced slightly to the left or right. L.M.'s judgment of the apparent motion in these stimuli exceeded chance only over a restricted range of spatial displacements. Also, her performance deteriorated rapidly with frame durations of <500 ms, whereas normal subjects do well with exposures of much more than 100 ms. However, inter-stimulus intervals (ISIs) of >40 ms degraded performance both for L.M. and for normal subjects. Since this latter behaviour characterizes 'short-range' motion mechanisms, the authors inferred that the 'residual motion perception in L.M. is carried out by short-range mechanisms'.

Trouble separating signal-from-noise

Unfortunately, the two-flash RDC used by Hess *et al.* (1989) contain spurious spatiotemporal frequency components (noise) which might have interfered with the perception of motion (Baker *et al.*, 1991). Conversely, the frame durations of 500 ms or more at which L.M. 'saw' motion might permit indirect inference of motion by scrutiny of random-dot clusters, another case of 'seeing' motion mediated by non-motion processes. Consequently, to improve the estimates of residual motion processing abilities in L.M., Baker *et al.* (1991) used several additional versions of random limited lifetime RDC stimuli. A 'Movshon noise' stimulus plotted spatially random 'motion' dots every 200 μ s over a total stimulus duration of 1000 ms. Between frames, a dot would 'live' or 'die' with a certain probability or 'coherence value'. A dot that lived was replotted a specific distance to the left or right of its previous location; one that died was replotted at a new random location. Using this procedure, Baker *et al.* (1991) found that L.M.'s lesions caused a tremendous increase

in the signal needed for L.M. to determine the direction of global flow compared with that needed by normal subjects. Surprisingly, when the motion stimulus used stationary dots for noise, L.M. displayed a severe defect over a range of lifetimes and displacements. To explain this result, Baker *et al.* proposed that stationary dots might effectively reduce the contrast of motion signal dots even though L.M. has near normal CS for static stimuli.

Effects of dot noise and lifetime were also examined using more explicit definitions of 'signal' and 'noise'. When signal dots jumped together for a specific number of frames (a lifetime) and noise dots jumped to new random locations in each frame, L.M.'s performance declined precipitously as noise was added, even for longer dot lifetimes. To determine whether the trouble was due to decreased signal or increased noise, L.M. viewed an identical display void of noise dots ('invisible noise') wherein the notion of low coherence refers to a decreased number and density of signal dots. The results showed dramatically better performance extending down to low dot densities. Additionally, when the effects of dot lifetimes were assessed at 100% coherence, L.M. had trouble for short dot lifetimes, but not enough to account for her trouble on the motion noise experiment. In other words, L.M.'s deficit was due more to trouble handling degradation by noise, than to trouble perceiving short lifetimes.

Specific aims

The current study follows up on the issues raised by previous studies of L.M. and also examines several additional questions to better characterize the perceptual deficits and mechanisms affected in cerebral akinetopsia. We have four specific aims.

(i) *To test the hypothesis of Baker et al. (1991) that cerebral akinetopsia is preceded by an inability to extract signal-from-noise.* To address this issue we evaluate the perception of global coherent motion and direction discrimination in L.M. using random-dot stimuli constructed with background noise. The stimuli in Experiment 1 are similar to the limited-lifetime random-dot stimuli used by Baker *et al.* (1991) but provide a more precise definition of signal and noise and use a single dot movement speed. Other data relevant to this hypothesis are collected in Experiments 2 and 3, which vary the signal-to-noise ratio in tasks of 2-D and 3-D object perception.

(ii) *To test the perception of 2-D shape-from motion and 3-D SFM in cerebral akinetopsia.* There is ample evidence that the visual system can use motion cues to extract information on 2-D figure-from-ground (Frost and Nakayama, 1983; Regan and Beverley, 1984; Braddick, 1993; Stoner and Albright, 1993) and even 3-D kinetic depth (Wallach and O'Connell, 1953; Braunstein, 1962). We hypothesize that the global motion processing disturbance in cerebral akinetopsia should also impair these perceptual abilities. Experiment 2 evaluated the perception of SFM using dynamic random-dot and random-line depictions of 2-D and 3-D objects. Experiment 3 evaluated the perception of 2-D shapes

using a letter identification task in which the letter targets were defined by motion, luminance transients, static or dynamic stereopsis, or differing static textures.

(iii) *To test if cerebral akinetopsia affects visuoperceptive abilities other than motion.* Relevant evidence on this issue was collected in Experiment 3 as well as in Experiment 4 which used a battery of standardized tests of static visuospatial perception.

(iv) *To evaluate the abnormalities in the apparent (ϕ) motion perception previously reported in L.M. (Zihl et al., 1983).* We were interested in the hypothesis of Baker *et al.* (1991) that L.M.'s trouble reflects an impairment of 'long-range' rather than 'short-range' mechanisms (Braddick, 1980). We addressed these issues in Experiment 5 by varying the inter-stimulus interval between the presentation of two frames in a bistable apparent motion stimulus known as the Ternus display (Pantle and Picciano, 1976). We also wanted to determine the relative contribution of the long- and short-range apparent motion systems to the bistable percepts experienced with this display.

General methods

Subject

The case of experimental subject L.M., a right-handed woman who had a secondary education, is fully described in previous articles (Zihl *et al.*, 1983, 1991; Hess and Baker, 1989; McLeod *et al.*, 1989; Baker *et al.*, 1991; Long, 1992). In brief, L.M. is now in her early fifties, and well adapted to her visual deficits. These deficits are the sequelae of cerebral infarction in 1978, probably due to venous sinus thrombosis. L.M. has no known underlying systemic disorder to explain her problem, and has had no new cerebral infarctions to the time of testing. She is intellectually intact apart from her vision impairments, and subsequently has been able to adjust to the demands of daily life, including widowhood. She lives independently in her own apartment, makes her own decisions, and leads an active social life, although she has not been able to return to her premorbid activity of running an electrical shop. L.M. negotiates stairs, and even rode the underground by herself, to participate, with her consent, in a week of experiments. She learned the faces of her new examiners (M.R. and M.N.) after first exposure, and recognized them days later, even out of context, from visual cues alone.

Experimental procedures

The procedures for Experiments 1–5 are outlined in Table 1. In testing L.M., we took the approach of Hess *et al.* (1989) and Baker *et al.* (1991) in that most tasks used an alternative forced choice (AFC) psychophysical procedures. Whenever possible, stimulus duration was unrestricted to avoid assumptions on L.M.'s short-term memory needed for AFC procedures, or focal attention needed for brief exposures.

Table 1 *Experimental procedure*

Experiment 1. Perception of a global coherent motion direction.

Experiment 2. Perception of SFM.

Screening: identification of 3-D SFM figures depicted rotating about the an axis (random-dot spheres, cubes, and a random-wire figure) versus non-figure foils (2-D and 1-D random noise in a circular aperture, a coherent sheet of moving dots, transparent limited version of 2-D random noise).

Experiment 2A. Identification of 3-D shapes amidst varying levels of background noise.

Experiment 2B. Perception of dynamic stereopsis.

(i) Perception of stereoscopically presented random-dot or random-wire figures rotating about their vertical axis (a sphere, a cube, a cube canted onto a corner to look like a diamond, and a random-wire figure).

(ii) Perception of stereo versions of the low-, medium- and high-noise stimuli from Experiment 2A.

Experiment 3. Perception of 2-D letter shapes from motion and non-motion cues.

Experiment 3A. Relative motion cues.

Condition 1. Letters defined by stochastically moving a proportion of dots falling within the letter region against a static random-dot background at different proportions of signal.

Condition 2. Like Condition 1, except stationary dots removed from background.

Experiment 3B. Transient cues—letter shapes defined by ‘on’ and ‘off’ transients falling within the letter region against a static random-dot background at different proportions of signal.

Experiment 3C. Static texture cues

Condition 1. Letter shapes differentiated from background by orientation of line segments.

Condition 2. Letter defined by small triangles against oriented line segments.

Condition 3. Letter shape defined by differences in dot density.

Experiment 4. Visuoperceptive tasks.

(a) Rey–Osterreith Complex Figure Test—copy and matching versions

(c) Benton Visual Retention Test—Revised. Form C and recognition versions F and G.

(b) Hooper Visual Organization Test.

(d) Mooney’s Closure Faces Test.

(e) Cookie theft picture.

Experiment 5. Perception of bistable movement with the Ternus display.

Data were collected in short sessions with frequent intervals of rest. Successive blocks of data were accumulated to yield psychometric functions for the different tests. All stimuli, except for those in Experiment 4, were generated by an Apple Macintosh computer and presented in black and white on a monochrome monitor at 100% contrast (white 19.5 cd/m²; black 0.0 cd/m²). The viewing distance was 57 cm. Stimuli were also viewed in similar conditions by normal control subjects with no cerebral lesions.

Experiment 1: perception of a global coherent motion direction signal

The study of motion perception requires a psychophysical stimulus and task design that relies exclusively on the perception of movement. An observer’s ability to infer movement from noticeable changes in the visual scene, the way we ‘see’ movement in the hands of a clock, or between two successive photographs, must be eliminated. For such reasons, we test motion perception using computer generated animation sequences known as RDC. These stimuli present a motion signal among spatially random background noise, allow variation of spatial displacement and temporal intervals at programmable exposure durations, and provide a more

objective measure of residual motion perception than do measures of D_{\max} or D_{\min} .

Random-dot cinematograms depict a number of small dots moving around within an imaginary aperture upon the computer screen. While a proportion of the dots move in a single, cardinal direction (signal dots), the other portion moves randomly (noise dots). When the proportion of randomly moving noise dots is low, the entire stimulus appears to have a global flow in the direction of the unidirectional signal dots. In this case it should be easy to determine the direction of signal dot movement. However, as the proportion of noise increases, the perception of global flow decreases, and it becomes more difficult to determine the direction of signal dot movement. Motion perception can be assessed by determining the proportion of signal necessary for the perception of the global movement. A larger proportion of signal indicates that the motion processing mechanism is less able to integrate the local motion vectors from the local dot movements into a global coherent motion flow. Therefore, a high threshold for direction discrimination indicates a disruption in the neural mechanisms for normal motion processing.

In Experiment 1, we attempted to confirm the Baker *et al.* (1991) result using an experiment including more directions

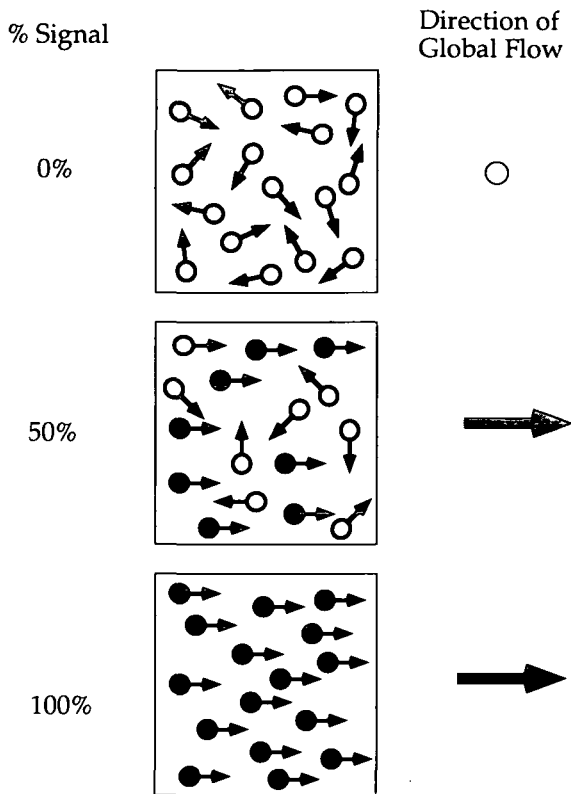


Fig. 1 The random-dot motion stimuli were composed of randomly positioned dots moving at a uniform speed. Signal dots, depicted black here, move in one particular direction (rightward shown). Noise dots, depicted white here, make up a flat distribution of movement directions so that their net movement is zero. Net or global stimulus movement is influenced by the proportion of signal to noise dots, with greater movement perceived with a higher signal proportion.

of movement and a more precise signal and noise definition whereby each stimulus comprised a single dot movement speed.

Method

Each RDC animation sequence contained up to 30 frames depicting 150 randomly placed, small (2×2 min) black dots moving within a $4^\circ \times 4^\circ$ square area. To generate the dot movements, each dot was displaced a small constant distance between cinematogram frames. The direction of this displacement came from one of two different distributions. A proportion of dots was given a unidirectional displacement. These displacements were either upward, downward, leftward or rightward and they gave the signal direction to the stimulus. The remaining dots were given displacements from a flat distribution of directions spanning all 360° . This generated the noise in the stimulus (see Fig. 1). The subject's task was to indicate the direction of global coherent motion, which should be determined by the direction of the signal displacements. The proportion of signal depicted in the motion stimulus was the main independent variable. Remember that

smaller proportions of signal made the direction discrimination task more difficult.

The perception of coherent motion, and, therefore, correct responses on the experimental task, depend on a motion processing mechanism's ability to integrate local motion cues across the display. This task cannot be completed by scrutiny of individual dots or groups of dots since the dots were small, frame and stimulus durations were brief, and the assignment of dots to a signal or noise distribution displacement varied between frames. A low dot density minimized the possibility of accidental correspondence between signal and noise dots on successive RDC frames (Williams and Sekuler, 1984) and similarly prevented a range of noise velocities which gives unreliable masking of the motion signal by the noise signal (Bravo and Watamaniuk, 1992).

Subject L.M. viewed the computer display from 57 cm while seated in a dimly lit testing room. Trials were initiated by the experimenter only after L.M. fixated a small cross at the screen centre. The RDC was presented in the centre of the screen and L.M. had to indicate which direction of signal motion was displayed.

A 'warm-up' and learning phase was implemented in two steps. The first step was to present a group of 15 small ($24' \times 10'$), like oriented, arrows to determine if L.M. could report their uniform direction with brief stimulus presentations. The second step used RDC stimuli ranging from 90 to 100% to determine if L.M. could perform the motion perception task. The ratio of signal to noise dots was varied within a method of constant stimuli. The experimental phase followed and used RDC stimuli ranging from 10 to 100% signal. By varying the dot displacement ($6'$ and $10'$) and frame rate (30 and 15 ms), two speeds were tested, $3.3^\circ/\text{s}$ and $11^\circ/\text{s}$, respectively. These tests were completed with brief stimulus durations varying from 450 to 195 ms in different conditions. L.M. completed 24 trials in each step for each of the two speeds tested. Responses were verbal or gestural and were recorded on the computer by an experimenter.

Results

First, L.M. was able to determine accurately the direction indicated by the static arrow cues with the brief 450 and 195 ms stimulus durations (94 and 82% correct, respectively). This demonstrates that L.M. had no overt behavioural deficit that precluded testing with this particular paradigm. Second, L.M. was able to detect motion direction at the high proportions of signal presented in the warm-up and learning phase (e.g. 94% correct in the $11^\circ/\text{s}$ condition). This demonstrates again that L.M. has no difficulty with this particular motion testing paradigm.

Data from each of the short testing blocks were compiled to generate one data set per condition. Thresholds for direction discrimination were determined by a probit analysis. Figure 2A demonstrates the threshold calculation with the

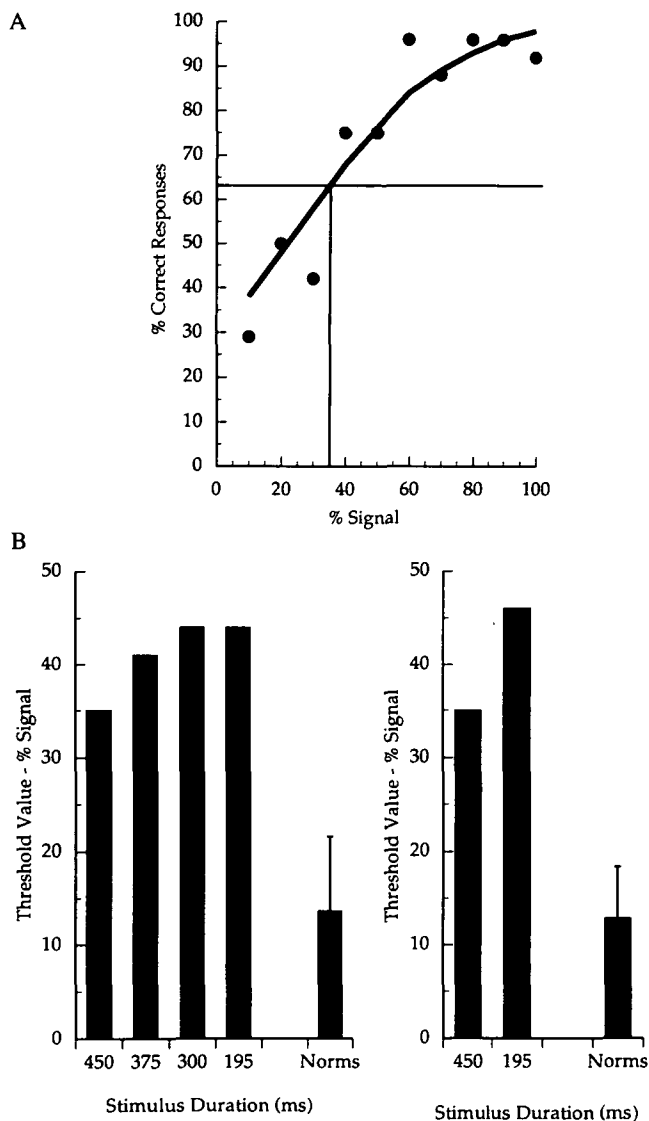


Fig. 2 (A) L.M.'s performance in the 11°/s and 450 ms condition of the direction discrimination task. The solid line shows the best-fit psychometric function. The value of this function at the point where it crosses statistical discriminability (horizontal line) is used to determine the percent signal at L.M.'s threshold for direction discrimination (vertical line). (B) *Left*, L.M.'s thresholds for various stimulus durations in the 3.3°/s condition; *right*, the thresholds for the 11°/s conditions. The performance of normal controls ($n = 22$, mean age 70 years) are shown for comparison. Error bars denote 2 SDs. The results confirm that L.M. has a persistent and severe motion direction discrimination deficit (Baker *et al.*, 1989).

arbitrarily chosen 11°/s, 450 ms condition. In this condition, L.M. requires ~35% signal dots to determine correctly the direction of signal dot movement. Thresholds were similarly determined for other conditions and for normal controls.

Results from the experimental phase confirm that L.M. has a persistent and severe motion direction discrimination deficit, similar to what Baker *et al.* (1991) showed. In both the 3.3°/s and 11°/s conditions L.M. needed ~40% motion signal to determine consistently the direction of signal dot

movement (Fig. 2B). Thresholds for older normal subjects are ~15% signal for a 195 ms presentation duration. L.M.'s thresholds are >5 SDs above normal.

Discussion of Experiment 1

Baker *et al.* (1991) hypothesized that L.M.'s performance deficit was due to decreased number of neurons carrying directional information or an impairment in processing stimuli with low signal-to-noise ratio. This led us to test the motion direction discrimination performance in L.M. by using RDC stimuli that provided a more precise definition of signal and noise. Our objective in Experiment 1 was to minimize any accidental correspondence between signal and noise dots which might produce a false low assessment of L.M.'s motion direction discrimination ability and to further reduce any non-motion cues which might allow correct inferences of global motion direction.

Like the earlier stimuli of Hess *et al.* (1989) and Baker *et al.* (1991), our RDC depicted small signal and noise dots moving within a circumscribed square target area. Also, since ISI was equal to frame duration time (15 ms) and each animation sequence contained up to 30 frames, overall stimulus duration of ~500 ms fell squarely in the range of residual motion performance in L.M., determined by Baker *et al.* (1991) as did the size of the dots and amplitude of dot displacements we used.

However, unlike those earlier stimuli, the RDC in the current study varied the assignment of a dot to the signal or noise distributions between every frame. This made it more difficult to follow the successive jumps of a single signal dot and maximized the likelihood that a correct response depended on the ability to pool the local directional motion cues across the stimulus. As our dots randomly switched between expressing signal and noise information in different frames, most signal dots in our RDC had short lifetimes, particularly at low percentage signal coherence. However, Baker *et al.* (1991) had already demonstrated a limited importance of dot lifetime compared with dot noise effects.

L.M.'s results using our stimuli showed the presence of severe motion discrimination deficits, resembling the findings of Baker *et al.* (1991). Using a similar paradigm in monkeys, Newsome and Paré (1988) found that the proportion of signal needed for such a task increased significantly when monkeys were given acute lesions to area MT. The MT lesions disrupted cortical motion processing in the monkeys, producing a performance deficit in the psychophysical task.

However, we did find residual motion direction discrimination in L.M. at the 11°/s velocity, higher than was expected. Moreover, at a quantitative level, our results show a less severe deficit with a threshold of 40% signal compared with the 80% thresholds measured by Baker *et al.* (1991). Consider also that normal thresholds were different: ~15% in our study and only 4% in the Baker *et al.* (1991) study. These differences indicate at least two things: (i) that the non-correspondence of velocity or spurious masking of signal

by motion dots played some role in the signal from noise deficit measured by Baker *et al.* (1991); and (ii) that while L.M. does have a severe motion perception deficit, she has considerable remaining motion vision, even more than Hess *et al.* (1989) and Baker *et al.* (1991) found. As a consequence, we wondered if this residual motion perception might be used to recover SFM or whether this ability was lost with cerebral akinetopsia. This is examined in the next experiment.

Experiment 2: perception of SFM

The perception of depth or SFM is one commonly cited ecological use of motion perception (Gibson, 1950; Nakayama, 1985). Since L.M. demonstrates a remarkable impairment in the perception of movement, we wondered if she might also show deficits in the perception of depth or structure from motion. Several earlier findings in L.M. suggested this might be the case. First, L.M. could not sense movement-in-depth on viewing a black cube moved toward or away from her and reported seeing changes in position but not velocity (Zihl *et al.*, 1983). Secondly, the spiral after-effect elicited no sense of motion-in-depth. Thirdly, we note with great interest the findings of Baker *et al.* (1991) in their experimental manipulations of dot noise in a motion direction discrimination task using RDC comparable to the task we used in Experiment 1. L.M. saw motion at 100% coherence but her performance rapidly declined (*see* Baker *et al.*, 1991; fig. 4, p. 457). Owing to the design of their stimulus, in the high percentage coherence range where L.M.'s performance declined, normals easily saw two transparent surfaces that were separated in depth. L.M., however, did not perceive this kinetic depth (incidentally, these cues were not available in the motion stimuli we used). Thus, Baker *et al.* (1991) produced a very important, if unintended, demonstration of possible abnormal SFM in L.M.

Screening procedures—identification of 3-D SFM figures among non-depth foils

In preliminary testing, L.M. correctly identified several 3-D SFM figures presented among several non-depth foils. Computer generated SFM figures were presented in orthographic projection on the face of the computer monitor. The figures included: transparent random-dot spheres, opaque random-dot spheres, random-dot cubes (lying flat or standing on a vertex), and a multisegmented 'random-wire' figure. The figures were shown rotating about either the horizontal or vertical axes. The non-figure foils included: 2-D random noise within a circular aperture, 1-D random noise in a circular aperture, a coherent sheet of moving dots, a pair of transparent random-dot sheets moving across each other in opposite horizontal directions, and a directionally limited version of 2-D random noise. As discussed in detail below, some of these foils may elicit a report of non-rigid structure or depth between the different directions of dot movement.

Part of the design was to determine whether L.M. would spontaneously generate such reports. Each of these stimuli was presented continuously until L.M. gave a response.

L.M. could readily report the structure of the SFM figures, similar to the patient A.F. of Vaina *et al.* (1990) who gave an accurate report of the structure of a rotating cylinder at high signal coherence. L.M. effortlessly described the spheres and cubes as voluminous objects and described the random line figure as rigid object resembling 'a bunch of rotating triangles'. L.M. reported that these figures appeared solid and to have depth. Of equal importance, L.M. did not report seeing a rigid 3-D structure in the presentations of the foils and saw no depth or structure in viewing the 2-D noise. She accurately described the pair of random-dot sheets, but did not report perceiving any depth between them.

While some normal observers report seeing a gelatinous sphere interspersed with dots in the 1-D random-noise display (Williams and Phillips, 1987; Treue *et al.*, 1991), or a barber's pole rotating and moving upward in the directionally limited 2-D random-noise display (Williams and Phillips, 1986), L.M. did not. The 1-D random-noise display is a random-dot display wherein dots can move randomly back and forth along one dimension, for instance, horizontally. In the directionally limited 2-D random motion, dots move randomly in directions 65° either side of upwards. In these cases, the perception of a rigidly rotating figure has been taken to suggest cooperative interactions among velocity-selective motion processing mechanisms (Williams and Phillips, 1987). L.M.'s inability to perceive depth or form in these stimuli underscores her inability to integrate stochastic motion information over space. However, in more orderly displays, L.M. has no difficulty in recovering 3-D SFM. The following experiments more closely examine L.M.'s perception of SFM in stimuli with a varying noise component.

Experiment 2A: two-AFC shape identification with varying amounts of background noise

Method

For an objective test of L.M.'s ability to perceive SFM, we developed a two-AFC shape identification paradigm where the observer had to report the shape of the object presented in each particular trial. Accurate performance on this task depends on the subject's perception of the figure's shape from motion. To prevent shape identification from non-motion cues, such as edges or dot density, and also to index the difficulty of the task, varying amounts of random-dot noise were added to a square background region surrounding the target.

The SFM figures were a random-dot sphere and a random-dot cube canted 45° about the *x*- and *z*-axes so as to stand on a corner. The figures rotated about either the horizontal or vertical axes. The two stimuli were of comparable size (~2.8° visual angle in diameter) but could be easily distinguished by the SFM cues in low noise conditions. These

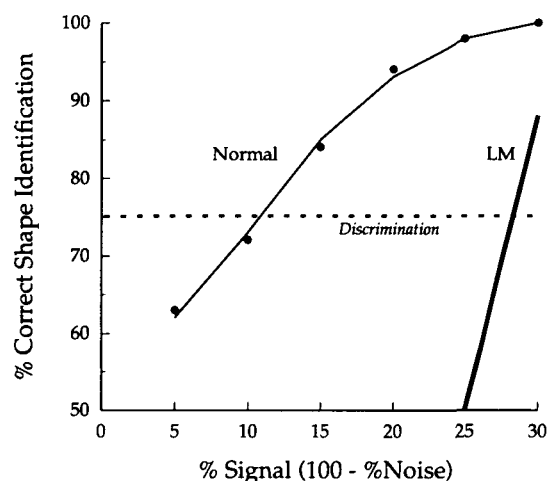


Fig. 3 For the kinetic depth shape discrimination experiment, normal discrimination performance is shown by the filled circles and the best-fit psychometric function. Normal threshold is at ~11% signal. L.M.'s performance is shown by the bold line. Her performance fluctuated at about chance (50% correct) but her psychometric function shows evidence of shape discrimination by 30% signal where performance exceeds 75% correct (dotted line).

figures were presented against a square background region $8^\circ \times 8^\circ$ visual angle. Within this background region either 20, 200 or 1000 small ($2' \times 2'$) white dots were presented, giving a nominal dot density of <1, 3 or 16 dots/square degree. Noise dots moved with a speed of $\sim 3^\circ/\text{s}$, which is approximately the speed that figural dots moved when fronto-parallel to the observer.

The signal to noise ratio of dynamic random-dot elements comprising the figure and background noise were varied. The low (10%) noise stimulus had 200 figure dots and 20 randomly moving noise dots comprising the background. The medium (50%) noise stimulus had 200 figure dots and 200 randomly moving background noise dots. The high noise (70–95%) condition had a 1000 noise dot background and a SFM figure composed of 50–300 dots.

In the low, medium and high noise conditions, L.M. was given four presentations of each of the two shapes (cube and sphere) rotating about each of the x - and y -axes. This gave 16 observations in the low and medium noise conditions and 48 observations in the high noise condition (six signal levels between 5 and 30%). In each presentation, the subject viewed one complete revolution of the figure, depicted in 180 sequential cinematogram frames presented with a 30 ms frame rate. The stimulus presentation lasted 5.4 s. Within each condition, stimuli were presented in a predetermined random order.

Results

With only 10% noise in a sparse 220 dot display and 50% noise in a 400 dot display, L.M. performed at 100% discrimination between the two shapes. However, with a higher dot density, and fewer dots defining the object, L.M. performed poorly. Figure 3 shows L.M.'s performance and

the performance of normal controls ($n = 8$, mean age 62 years). Normal threshold level for discrimination, shown with the horizontal line at 75% correct, is slightly more than 10% signal. In contrast, L.M. did not begin to discriminate reliably between the two SFM figures until the signal was near 30%. This is a significant threshold elevation compared with normals. The high stimulus noise and low stimulus signal in this set of stimuli severely affects L.M.'s ability to recover SFM. Of course, it is important to note that in less noisy conditions, L.M. performs normally. Unless the stimulus is obscured by a high proportion of noise, L.M. has no difficulty perceiving SFM.

Experiment 2B: dynamic stereopsis

The perception of structure in a moving display is aided by binocular disparity cues. The perceived depth magnitude of displays containing both disparity and SFM is reported to be much greater than perceived with either of these cues alone (Tittle and Braunstein, 1993). Considering that L.M. has only marginal static stereo acuity (140 min measured with the Randot stereotest) and shows some deficit in the perception of SFM in noise, we wondered if L.M.'s performance in the previous shape discrimination task might be aided by the addition of disparity information (Rouse *et al.*, 1989). Alternatively, it is possible that L.M.'s deficits in motion perception and static stereopsis might also include dynamic stereopsis. In this case disparity information would not confer an advantage for the perception of SFM. To address L.M.'s use of dynamic disparity information, we examined whether L.M. could use dynamic stereopsis for: (i) disambiguating the direction of rotation in an otherwise rotationally ambiguous SFM figure; and (ii) improving performance on the high noise condition of the shape identification task used previously. In the second condition, binocular disparity information should make the noise dots appear at a plane behind the rotating figure. With this depth separation between signal and noise, figural discrimination should be easier and performance improved compared with the condition of motion alone.

Method

In both conditions, computer generated figures were viewed through a liquid crystal stereoscopic shutter system. This stereoscopic viewing system allowed the presentation of different views to each eye as alternating stereo frames were drawn to the computer screen. The alternating frames had slightly different views of the stimulus display. Although the frames were presented asynchronously to the two eyes, this system generates the essential disparity conditions necessary for binocular stereopsis.

In the first experiment, L.M. viewed several stereoscopically presented random-dot or random-wire figures rotating about their vertical axis. The figures were a sphere, a cube, a cube canted onto a corner to look like a diamond,

and a random wire figure (Nawrot and Blake, 1991b). The relative disparity between the front and rear surfaces of the figure was 4', 8' or 12', or the front and rear surfaces had 2', 4' or 6' crossed and uncrossed disparity, respectively. By virtue of the disparity information, the previously ambiguous rotation of these SFM figures is rendered unambiguous: the disparity information specifies a particular depth arrangement in the stimulus and therefore a particular direction of rotation. L.M.'s task was to indicate the direction that the figure appeared to rotate. From this response we can determine which surfaces of the figure were perceived as front and rear, and whether this corresponds to the disparity information presented in the stimulus.

In the second experiment, L.M. viewed stereoscopic versions of the low-, medium- and high-noise kinetic depth stimuli described earlier in this experiment. The stimulus parameters were essentially identical, with the same dot numbers, densities and stimulus sizes. Again, white dots were presented against a black background. For the stereoscopic presentation, two stereo-pair animation frames were generated for each figure position in the animation sequence. First, background dots were given 6' of uncrossed binocular disparity so that all the noise dots appeared on a plane behind the random-dot figure. The dots on the plane still move about randomly on the plane, but did not move in and out of the plane in depth. Secondly, dots defining rotating figure were drawn with varying amounts of binocular disparity such that the front surface of the figure had 6' crossed disparity, the rear surface 6 min uncrossed disparity, and a smooth continuum in between along the surface of the figure. Again, the disparity information defined two different directions of rotation about either the *x*- or *y*-axis. Figure 4 illustrates how the random-dot figures appeared in front of a plane of noise dots. Of course, in the actual experiment the figure rotated, and the noise dots moved randomly about their plane.

In all conditions, L.M. viewed one rotation of the figure, which gave a stimulus presentation duration of 5.4 s. Using the liquid crystal display (LCD) shutters, each eye was presented their respective frame of the stereo pair for 15 ms, while the other eye was occluded. An entire stimulus comprised 360 frames, of which each eye viewed only their respective 180 frames.

In the first direction of rotation condition, L.M. viewed 16 figures with each of the three amounts of disparity for 48 presentations total. In each of these presentations, L.M. had to signal the direction that the figures appeared to rotate. In the low- and medium-noise conditions, L.M. viewed 16 presentations of the various stimuli (two trials for each shape, axis and direction of rotation). In the high-noise condition, L.M. viewed 24 presentations with only the *y*-axis of rotation. In this experiment, L.M.'s only task was to identify whether a cube or a sphere shape was being presented.

Results

L.M. reported little appreciation of a solid 3-D object in the dynamic stereopsis displays. She showed 0% rotation

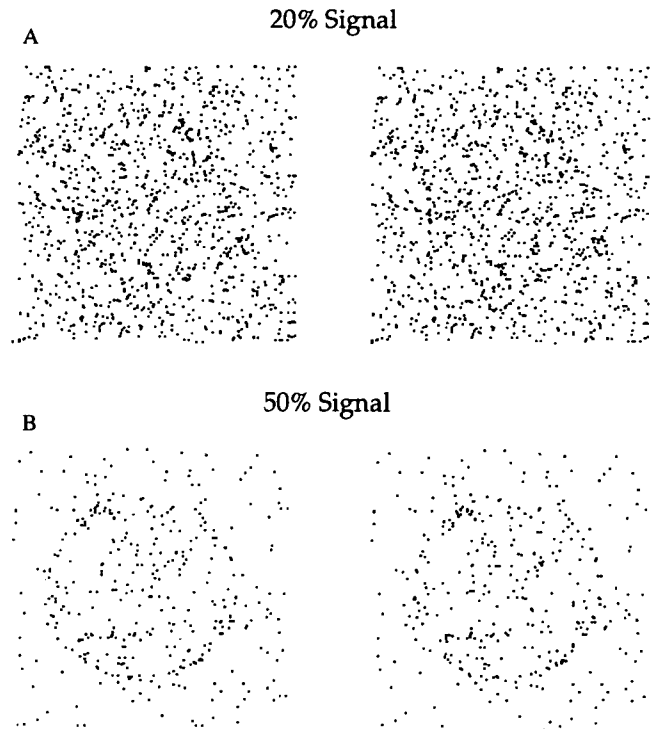


Fig. 4 For the binocular stereopsis shape discrimination experiment, a spherical or cubic shape was hidden amongst a background of noise dots. With binocular viewing the figures appear in front of the noise and the shapes are easily discriminated. For illustration, the stereo-pairs here may be viewed with crossed eyes (free fusion) for appreciation of the depth and shape discrimination task used in the experiment. (A) A cube depicted with 20% signal dots and 80% noise dots; (B) a sphere depicted with 50% signal dots and 50% noise dots.

direction discrimination for all disparities tested. In all trials of the first experiment, L.M. reported that the front of the figure was moving leftward (clockwise rotation of the figure in top-view). The disparity cue had no effect on the reported direction of rotation. We noted in further testing, however, that L.M. reported spontaneous reversals in the direction of figural rotation of a (non-stereoscopic) SFM figure when presentation durations were 15 s or longer. In other words, like normals, L.M. can perceive both rightward and leftward rotation in SFM figures. She is simply unable to use dynamic binocular disparity information to disambiguate direction of rotation.

In the stereoscopic version of the shape identification task, L.M.'s performance was similar to that in the kinetic depth version. L.M. had no trouble identifying the objects in the low- and medium-noise version of the task (100% and 88% correct, respectively). In the high-noise version of the test, L.M.'s managed reliable discrimination between the objects at 30% signal. This is similar to the threshold obtained in the kinetic depth stimulus in Experiment 2A. In other words, the addition of dynamic disparity cues in this experiment failed to convey any advantage in the perception of 3-D form. As the information from the kinetic depth experiment was available and L.M.'s performance was similar, motion

information must have been the sole source of shape information that L.M. used. Therefore, it appears doubtful that L.M. uses dynamic stereoscopic information in the perception of depth.

In an ancillary test of L.M.'s use of binocular disparity information, L.M. was presented with a static stereoscopic version of the medium noise stimuli using the LCD shutter system again. Here, with 16 presentations again, L.M.'s discrimination performance dropped to 69% correct. With a two-alternative force choice procedure, this is only 38% discrimination. Normal discrimination is near 100%. Therefore, it appears that while L.M. has difficulty recovering SFM information, binocular disparity information conveys no additional benefit.

Discussion of Experiment 2

The ability to recover form- and depth-from-motion allows us to segment images into different objects at different depths based on relative movement. This perceptual ability is comparable in man and monkey (Siegel and Andersen, 1988), and probably depends on the operation of motion processing units in visual association cortex. In fact, a possible network for the processing of kinetic depth can be constructed from motion processing units whose properties are modelled after those of neurons identified in the monkey's area MT complex (Nawrot and Blake, 1991a). Damage to these processing units in primate area MT leads to errors in recovering shape-from-motion (Schiller, 1993). Consequently, it was important to examine the ability to recover form- and depth-from-motion in L.M. who has a well-documented motion perception deficit due to damage in neural units responsible for processing motion.

Based on the results of Experiment 2, we find evidence that L.M. does have residual perception of 3-D SFM. L.M.'s ability to identify rotating wire frame figures from successive 2-D projections is not simply a question of interpolating perceptual constancies from a number of learned 2-D retinal views. This is because she can perceive the volume even in a completely unfamiliar figure. Moreover, she can perceive 3-D volume from 2-D RDC displays in which there are no successive familiar views. However, the performance in L.M. is not normal for the same reason that she failed to perceive a directional motion stimulus in Experiment 1. Namely, her perception of 3-D form is very sensitive to the presence of noise amongst signal, which was evident when she had to identify a sphere or cube defined by moving dynamic random dots in Experiment 2A.

Comparisons with other cases

Aspects of the current findings in patient L.M. resemble those in patient A.F., who reportedly had bilateral lesions of the temporo-parieto-occipital junction (Vaina *et al.*, 1990) and could still perceive 3-D SFM despite other motion processing deficits, and appear to differ from the report of

four patients with right parieto-occipital lesions (Vaina, 1989) with total inability to perceive 3-D SFM. These latter patients failed to identify and name a 3-D object defined by the projection of randomly spaced dots lying on the surface of an imaginary rotating cylinder, which A.F. could still do. Instead of reporting a rotating cylinder they reported 'a bunch of dots moving', 'mosquitos or flies', 'birds high in the sky' (Vaina, 1989), 'snow blown by the wind', or 'ants crawling on the ground' (Vaina *et al.*, 1990). The findings were discussed in relation to the 'parieto-occipital' lesions in L.M. (Vaina, 1989; Vaina *et al.*, 1990); however, we find it difficult to make direct comparisons.

The seemingly worse performance on a 3-D SFM task in Vaina's right parieto-occipital patients may reflect several factors. First, the epoch of testing was only 6–9 weeks post ictus versus several years in L.M.: testing in the chronic phase generally shows some recovery. Secondly, there are issues of anatomy: the right parietal lesion localization in Vaina's cases relied on brain CT, but no images were published and no other localizing details were given. The lesions may have actually formed part of larger unilateral or even bilateral hemispheric lesions not detected by CT performed just after a cerebrovascular event, as was ultimately reported in A.F. A third factor is the design and implementation of the psychophysical task. Vaina tested her patients with only a single trial at one low signal density. The entire stimulus comprised only 16 random dots. Performance on more trials at higher densities may have revealed residual ability as we found in L.M.

A.F. was tested on multiple trials using a more sophisticated version of a rotating cylinder. The stimulus plotted 128 dots in a $3^\circ \times 3^\circ$ field. In one version, percent signal was varied at 400 ms dot lifetime. In a second version, stimulus duration (dot lifetime) varied at 100% signal. Compared with 11 control subjects, A.F. could perceive 3-D SFM, but this performance was sensitive to noise, and deteriorated at 42% signal or less, resembling the current findings in L.M. Performance in A.F. deteriorated below a stimulus duration of 400 ms, resembling the findings in the dot lifetime experiments in the motion direction discrimination experiments in L.M. by Baker *et al.* (1991). However, there are questions concerning the localization of the lesions that underlay the motion deficits in A.F. which hinder anatomical comparisons with the case of L.M..

A.F. was a 60-year-old left-handed man who had an acute right hemisphere haemorrhagic infarction by CT (unpublished), a dense left visual field defect for luminance and form, impaired visuoconstructive ability, and impaired static stereopsis, but preserved visual acuity, contrast sensitivity and colour discrimination. An MRI was obtained 3 months after the ictus and selected T₂-weighted transverse sections were reported to show bilateral lesions of the cortex at the temporal-parieto-occipital junction (Vaina *et al.*, 1990, p. 354). Yet, the published images (Vaina *et al.*, 1990, fig. 1, panels C–F, p. 355) show no lesion reaching the lateral surface of the left hemisphere. There is a haemosiderin

deposition in the right hemisphere consistent with chronic haemorrhagic changes, but the cortical component of the lesion is dorsal and posterior to the temporal-parietal-occipital junction and its location is mostly parieto-occipital (sections E and F). Most evident are bilateral patchy subcortical white matter signals consistent with A.F.'s history of long-standing untreated hypertension. Perhaps these lesions undercut white matter connections to and from a human MT (V5) homologue, as reported in a patient with a unilateral right hemisphere lesion (Rizzo *et al.*, 1992). Yet, A.F.'s right parieto-occipital lesion should have been sufficient to impair motion perception judging by the report of Vaina (1989). Consequently, why A.F. performed better on a 3-D SFM task than Vaina's four right parieto-occipital patients is puzzling, since A.F. also had a right parieto-occipital lesion. One possible explanation lies in the different 3-D SFM stimuli administered. Another possibility is that Vaina's (1989) patients had lesions that were more extensive than the initial CTs showed, similar to the pattern reported in A.F. based on the later MRI. In any case, A.F.'s lesions differ from L.M.'s in that A.F.'s were primarily subcortical and probably more diffuse.

Experiment 3: perception of 2-D shape from motion and non-motion cues

Having determined in Experiment 2 that L.M. has residual but deficient processing of 3-D SFM, we undertook to evaluate her ability to perceive 2-D shape from motion and non-motion cues. A great many visual cues provide information about 2-D shape. These cues include luminance, texture, colour and even motion boundaries. Of these cues, shape from motion is found to be compromised following posterior parieto-temporal brain lesions (Regan *et al.*, 1992). Given the location of L.M.'s cortical lesions and the extent of her motion perception deficits, we wanted to determine if her ability to detect 2-D shape from motion was likewise impaired.

Method

To minimize changing procedural demands on the observer, a single behavioural task was used to test the perception of 2-D shape from several different types of visual cues. The task, an adaptation of the procedure introduced by Regan and Hong (1990), was a simple five AFC letter identification. In each condition, a single independent variable (the proportion of a particular visual cue) was used to define a single letter amongst a background of noise. The letter shape was defined by texture, luminance, motion, motion direction, motion speed, luminance transients, and static and dynamic stereo (Nawrot *et al.*, 1995).

A dark square background region, $4.2^\circ \times 4.2^\circ$, was filled with 4000 randomly positioned $1' \times 1'$ white dots. Camouflaged within this background region was one of five letters, H, O, T, E or L. The length of each letter stroke was

2° and the width was 0.47° . Each letter was made from two, three or four of these strokes. All letters were block type and contained within a $2^\circ \times 2^\circ$ area which had five possible positions within the background region.

To make these letter-shaped areas visible, a local change in some particular aspect of the dots, or their movement, was applied to the otherwise random-dots falling within that area. For instance, movement of dots within the letter-shaped area makes the letter visible against the stationary dots in the background region. To reduce the utility of any incidental cues, letters could appear in the centre or offset 0.66° diagonally towards one of the corners of the background region.

In a warm-up and learning phase, L.M. could effortlessly identify black block letters against a white background in this experimental design with a 500 ms stimulus presentation. Given this performance for identifying simple letter shapes in brief presentations, it was clear that L.M. did not have attentional difficulties to interfere with her performance of this task.

Relative motion cues

Condition 1

Letters were defined by stochastically moving a proportion of dots falling within the letter region against a static random-dot background (Fig. 5A). The proportion of moving dots, % signal, was varied across trials between 70, 90 and 100% in a method of constant stimuli. L.M. completed 75 trials in this condition.

Results

Normal subjects require only 1% signal to perform the task accurately. L.M.'s performance was 32, 52 and 68% correct for the three signal levels. This gave L.M. a threshold of close to 100% signal for letter identification with this cue. Quite clearly, L.M. has a very significant deficit in the perception of 2-D shape from motion against a stationary background.

Condition 2

In condition 1 above, L.M. not only gave poor performance but also complained that the stimulus movement appeared 'troubling to look at'. To pursue this 'troubling' aspect of L.M.'s perception of the stimulus, we removed the stationary dots from the background region. Using only a signal proportion (moving dots) of 100% within the letter-shaped area, this new stimulus appeared to be a stationary letter-shaped aperture in front of a field of dots moving together in a single direction (Fig. 5B). The stimulus had a plain black background. L.M. completed 25 trials in this condition.

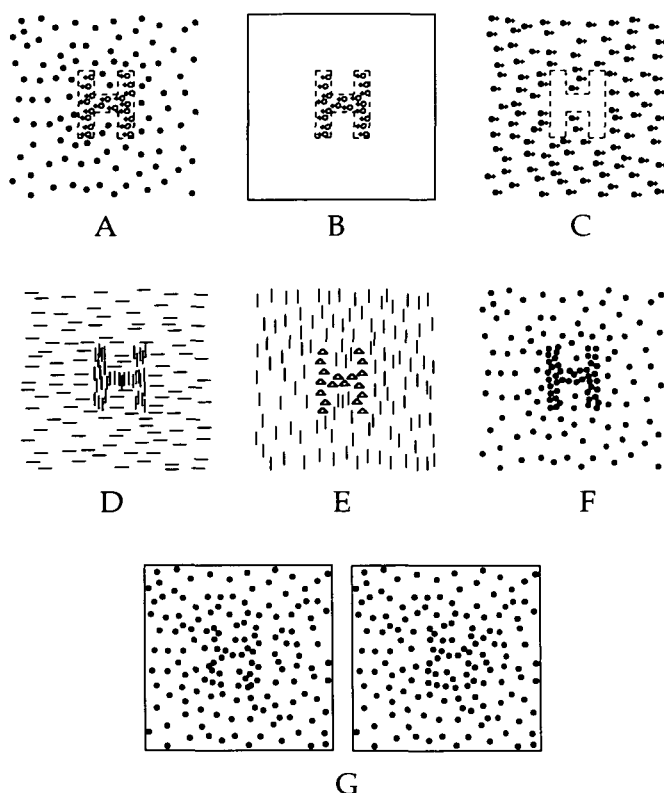


Fig. 5 Experiment 3 used several different shape-from-cue stimuli to examine L.M.'s ability to recover 2-D shape from motion and other cues. The letter shapes were made visible by: movement against a static background (A); movement against a blank background (B); a blank letter area against a moving background (C); different orientations of texture elements (D); different types of textures (E); different local dot densities (F); binocular disparity (G). A representation of depth in G may be seen by free fusing the pair of figures. An 'H' should appear in front of the background.

Results

Here L.M.'s performance improved compared with condition 1. She got 80% of the trials correct compared with 68% correct in the previous condition. As normal observers have no difficulty performing at 100% correct, this performance still indicates some difficulty in shape perception. Of course, a number of cues other than the movement of dots might be used for the identification of letter shape. For example, large scale luminance differences would have been an effective cue, as would be the accretion and deletion boundaries caused by the dots appearing and disappearing at the edge of the letter shape. It appears that the 'troubling nature of movement' was again a factor in L.M.'s performance; i.e. while L.M.'s perception of motion is clearly impaired, the mere presentation of a moving stimulus to L.M. interferes, at some level, with the processing of other visual information.

Condition 3

In the previous condition, movement within the letter-shaped area had an effect on L.M.'s ability to identify the letter

shape, even though stationary dots in the surround were removed. In another attempt to address this interesting aspect of L.M.'s perceptual difficulties, the contingencies of the previous experiment were reversed. Here the letter-shaped area remained blank, as if occluded, while dots in the background region moved together in one of the four cardinal directions (Fig. 5C). Like the previous condition, large-scale luminance cue and accretion/deletion boundaries could be used for letter identification. However, this stimulus had no dots or dot movement within the letter-shaped area to be identified. L.M. completed 25 trials in this condition.

Results

L.M.'s performance improved compared with the previous conditions to a near perfect 96% correct (one error). Her performance in this condition suggests that movement in the background region does not interfere with letter identification as does movement in the letter-shaped area itself. Since we assume L.M. was attending to the letter-shaped region, one possible explanation is an accompanying attentional deficit related to the perception of motion. Movement within L.M.'s focus of attention disturbs other visual processing, while movement in the surround may not. As we summarize below, this tenuous explanation requires more study.

Other conditions

Several other relative motion conditions were attempted with L.M. She was unable to perform the letter identification task when dots in the background and letter moved in opposite directions, orthogonal directions or at different speeds. L.M. simply found these conditions too difficult, and again too troubling to even complete the small number of trials required for each test.

Transient cues

This condition of the letter identification experiment used transient visual cues that did not have a movement component *per se* (Kulikowski and Tolhurst, 1973). The stimuli were similar to those used in the previous conditions. The background region was filled with 4000 randomly placed dots. An instantaneous accretion or deletion (in different conditions) was applied to a proportion of dots within the letter-shaped area. This addition or deletion of dots was applied such that the maximum dot density within the letter-shaped region was equal or lower to that in the background. To perform the letter identification task, the observer had to detect an instantaneous transient signal mid-way through the 500 ms stimulus presentation. Preliminary testing indicated that it was necessary to use a signal proportion (the proportion of dots appearing or disappearing) of 50%. L.M. completed 25 trials in each of the two conditions.

Results

Similar to the relative motion conditions, L.M. performed poorly compared with normal controls. With 50% of the dots within the letter region being deleted, L.M. performed at only 44% correct. She performed at 32% correct when the dots were being flashed on. The threshold for normal subjects is in the order of 2–5% signal. L.M.'s threshold could not be determined. At the high proportions of dot accretion or deletion needed by L.M., relative density cues were a significant confound. Her correct responses could have been based on static textural cues created in the background by the absence of a large percentage of dots either before (accretion case) or after (deletion case) the transient signal was applied. An ancillary condition with 70% signal, appears to confirm this as L.M.'s performance increased to 80% correct. L.M. could not use a non-motion transient signal for letter identification, but instead based her responses on relative density cues.

Static texture cues

While the warm-up condition with the black block letters demonstrated that L.M. could easily perform the letter identification task, the goal of these static non-transient control conditions was to determine whether L.M.'s trouble in the previous conditions are the result of a generic problem in isolating any type of signal in a noisy background.

Condition 1

Letter-shaped areas were differentiated from the background region by the orientation of line segments. The stimulus background was filled with 1000 small lines, $2' \times 12'$, all in either a vertical or horizontal orientation. Within the letter-shaped region, the orientation of a proportion of lines was changed by 90° (Fig. 5D). Like previous conditions in this experiment, a larger proportion of the signal in the letter-shaped region made the letter more easily identifiable. In this condition, the proportion of signal was set at 100% and the presentation duration doubled to 1 s. L.M. completed 50 trials.

Results

At 100% signal, L.M.'s letter identification performance of 26% correct was only slightly better than chance. Normal performance at 500 ms presentation duration is characterized by a threshold of ~32% signal, and near perfect performance at 100% signal. Therefore, in addition to her difficulties with moving and transient stimuli, L.M. also has difficulty in determining letter shape from texture differences from orthogonal line orientations.

Condition 2

Since L.M. had difficulty with letter identification from very simple texture boundaries, we wondered if her performance

would improve with a larger difference between the two textures. In this condition, the letter-shaped region was filled with small triangles ($10'$ per side). The element density was reduced by two-thirds to preserve the overall pixel density within the letter-shaped region thus avoiding a potential large-scale luminance cue. The background comprised the same oriented line segments of the previous condition (Fig. 5E).

The difference between these two textures is best understood in terms of Julesz's texton theory of texture perception (Julesz, 1986). The texture of a visual scene is analysed by the observer's array of textons. One type of texton might be simple non-overlapping line segments having a length, orientation and width. Another type of texton is a terminator (ends-of-lines). Yet another type of texton is a blob. In the stimulus used here, the letter-shaped region differs from the background in at least two textonal properties, the number of terminators, and blobs. First, the background line segments each have two terminators (ends) while the triangles have none. Secondly, the line segments making the triangles should also form blobs. Furthermore, the length and width dimensions of the lines and blobs differ considerably. Therefore, discrimination between the two textures could be based on a couple of different features, whereas in condition 1, it would be based on orientation alone. Would it make any difference in L.M.'s performance? Here, the proportion of signal was set 100% for every trial and the presentation duration was set to 1 s. Again, L.M. completed 50 trials.

Results

L.M.'s letter identification performance increased to 64% in this texture condition at 100% signal. L.M.'s improvement in this condition, compared with the previous condition, is most likely due to the additional information available through the different type of texture. Of course, her performance was still very different from normal.

Condition 3

In a final static texture condition, a dot density was used to generate a texture difference. First, the background region was filled with 4000 small dots, the same dot density as used in the relative motion experiments above. Within the letter-shaped region, the local dot density was increased in some proportion to the background region. A 100% increase would mean double density (Fig. 5F). Of course, local luminance differences mirrored the local density differences: a higher density of light dots generates a higher local luminance. The percent signal, local dot density as an increasing function of the background density, was varied according to the method of constant stimuli between 100% and 250%. Presentation duration was 500 ms. L.M. completed 100 trials.

Results

L.M.'s threshold in this density condition was 163% signal. This means that the density of dots within the letter region

had to be nearly 1.5 times the background density before L.M. could reliably discriminate the letter. The average normal threshold for age matched controls is in the order of 120%. The difference between L.M.'s performance and normal performance is very small in comparison to the size of the deficit L.M. exhibits in the other cue types in this experiment. The result from this condition shows that L.M. can perform the letter identification task if given a static luminance cue, even if it is made out of small dots. As long as the dots are not moving, she has less difficulty with the task.

Binocular disparity cues

To test letter identification from static stereopsis, a random-dot stereogram was generated. Background dots had zero binocular disparity. A proportion of dots within the letter-shaped region were given 6' crossed binocular disparity. The two frames of the stereogram were viewed alternately by the two eyes through a LCD shutter system linked to the 67 Hz vertical retrace of the monitor. The letters appeared to be made of dots closer to the observer than the background dots. In this condition, the proportion of dots within the letter shapes with binocular disparity was set to 100%. Figure 5G shows a static stereopair with 100% signal depicting an H in the centre of the stimulus. To give L.M. ample time for stereofusion with the LCD goggles, the presentation duration was 2.1 s. L.M. completed 50 trials in this condition.

Results

L.M. performed at only 12% correct, even though the stimulus was at 100% signal. Average normal performance is characterized by a threshold of 23% signal. Normal performance is typically perfect at 100% signal. Apparently, L.M. had trouble with letter identification when static stereo cues defined the shapes in the random-dot stimulus. This result confirms that L.M.'s does have some impairment of stereoscopic vision. While the disparity in these stimuli was above L.M.'s stereoacuity of 140', she was unable to group the dots into a structure she could identify as a letter shape. To further underline her difficulty with moving stimuli, L.M. was unable to complete testing when a moving version of this stereoscopic stimulus was presented. In this stimulus, the dots moved about randomly, but any moving to a position inside the letter-shaped area was given a crossed binocular disparity so that a scintillating letter appeared in front of a scintillating background of dots. L.M. found this stimulus too troubling to continue beyond a few trials.

Discussion of Experiment 3

2-D shape-from-motion

To summarize, L.M. had reduced ability to perceive 2-D shape from motion. She could easily read block letters, but threshold requirement was nearly 100% signal when the

letters stimuli were defined by moving dots among a static random-dot background compared with 1% signal for normals (Experiment 3A, Condition 1). This difficulty with 2-D shape perception in the presence of stationary noise resembles the pattern described in L.M. by Baker *et al.* (1991) of poorer perception of a directional motion signal in the presence of stationary noise. This signal-from-noise problem may even mask available stationary textural cues that could be used for 2-D shape identification, similar to the troubles that Merigan *et al.* (1993) reported in monkeys with area V2 lesions. Moreover, the masking effects are worse when the motion signal occurs within the boundaries of the target shape (Experiment 3, Conditions 1 and 2) than when in the surround (Condition 3), suggesting a link to L.M.'s focus of attention. Also, motion masks motion, whether the signal and noise are orthogonal or opposite to each other. A remaining challenge is to be able to explain these findings in terms of the known centre-surround properties of receptive fields of neurons in primates visual association cortex such as simian area MT (V5) and their additive and inhibitory interactions. We do not yet have the solution.

Perception of 2-D shape from non-motion cues

L.M. had difficulties perceiving 2-D shape from motion with cue types other than motion including transient cues, textures, and dynamic and static binocular disparity. The only condition in which L.M.'s performance approached normal was in the case of the texture density cue. Therefore, it is clear that L.M. can perform the task correctly, and even well in the case of a static luminance cue for 2-D shape. However, with most other spatial cues, L.M. showed severe deficits in recovering 2-D shape from these non-motion cues in the presence of noise (Merigan *et al.*, 1993).

Experiment 4: visuo-perceptive tasks

The results in Experiment 3 show that L.M. has trouble perceiving 2-D shape from non-motion cues. The question arises whether this form perceptual trouble in L.M. is restricted to 'early vision' tapped in Experiment 3, or whether higher order visual cognitive functions are also affected. To investigate this issue it would be necessary to present stimuli that tap higher order visual processes. As well, these stimuli must contain sufficiently high levels of signal to override the signal-from-noise deficit measured in previous experiments. This is analogous to using oversized letters to show that a person with low visual acuity still has preserved lexical functions. Thus, in Experiment 4 we used five different standardized neuropsychological procedures and their variations. All stimuli consisted of high contrast static black-and-white figures which are designed for viewing in a relatively wide range of ambient room lighting conditions. These tasks provided an index of L.M.'s 'visuoconstructive' abilities, referring to a combination of processes which allow

us to perceive all the features of a display and to judge the spatial relationships among those features.

Rey–Osterreith complex figure test (CFT)

This test requires subjects to copy a complex geometric figure. Good normative information is available (Spreen and Strauss, 1991). An extensive scoring system is provided, and response time is recorded as a second measure of subject performance. The CFT copy provides a reliable index of visuoconstructional ability, independent of memory function. We also administered a version of the CFT in which drawing is not required and performance depends on recognition rather than reproduction. This version uses 10 pairs of Rey figures. One member of the pair is always identical to the target item (the standard Rey figure) while the other differs with respect to a single detail.

Benton Visual Retention Test—Revised (BVRT)

The BVRT requires a subject to reproduce, by drawing, 10 line drawings depicting geometrical designs (Benton and Van Allen, 1985). Typically, the subject is shown each plate for 10 s, the plates are withdrawn, and the subject is asked to reproduce the figure by drawing on a white paper, after a 15-s delay. The first two designs consist of a major geometrical figure and the remainder contain two major figures and a peripheral figure. The BVRT is sensitive to impairments of visual memory, perception and visuoconstructive impairments. It is well standardized, and has three different, but equivalent forms (A, B and C). It is easy to administer, and takes ~10 min in most subjects. We administered form C. We also administered versions F and G of the task in which drawing is not required and performance depends on recognition rather than reproduction (Benton, 1990). The subject's task is to select which of four plates is identical to a previous drawing which was viewed for only 10 s. Versions F and G each contain 15 different items.

Hooper Visual Organization Test (HVOT)

In this task (Hooper, 1958; Western Psychological Services, 1983), the subject is asked to identify 30 different items (e.g. scissors, shoe, broom, fish) from cut up, rearranged line-drawings of those objects. This test is memory dependent since it depends on a history of exposure to the items represented in the test.

Mooney's Closure Faces Test

This test (Mooney and Ferguson, 1951; Lansdell, 1970; Newcombe, 1974) is a 'closure test' which provides information similar to the VOT. The subject is presented with 44 different black and white incomplete cartoons of faces. The subject is asked to judge the age and sex of the faces

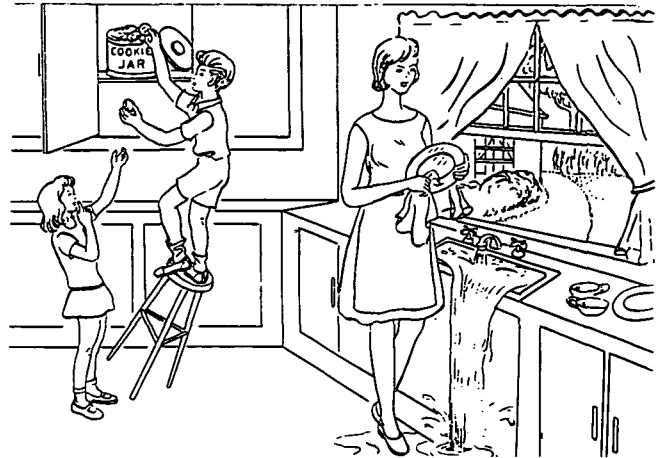


Fig. 6 The cookie theft picture. L.M. reported all the major items in this high contrast black and white line drawing, just as normal individuals do. She reported 'a scene' of 'a woman washing dishes', and the 'water running over'. She also saw 'a girl', 'a boy reaching and giving something to the girl' and noted the 'boy is in trouble because he is not allowed in the cookies' and 'will fall because the chair is falling over.' (Reproduced courtesy of Harold Goodglass.)

depicted. Performance on this task is memory dependent, but the recognition of previously familiar faces or famous faces is not required.

Cookie theft picture

This black on white line drawing of a complex picture from the Boston Diagnostic Aphasia Examination (Goodglass and Kaplan, 1983) is designed with a balance of information among the four quadrants and tells a story (*see* Fig. 6). The subject is asked to view the picture and report what they see. Scoring is qualitative and depends on a report of the major items in the display.

Results

Complex figure test

Despite liberal scoring, severe impairments were noted on two occasions (*see* Fig. 7). This included scores of four out of 36 at >10' and 8.5 out of 36 at >15'. Importantly, L.M. recognized that there were differences between the test figure and her own reproduction of it. We did not undertake to repeat the test for memory because of the poor performance to direct copy. However, when L.M. was administered the matching variant of this task, she performed much better. She matched nine out of 10 items correctly, albeit slowly (mean time per item: 71.2 s, SD 39.4). The performance of two female subjects aged 52 and 53 years was 100% correct and required 8.3 s (SD 2.5) and 7.5 s (SD 2.4) on average per item.

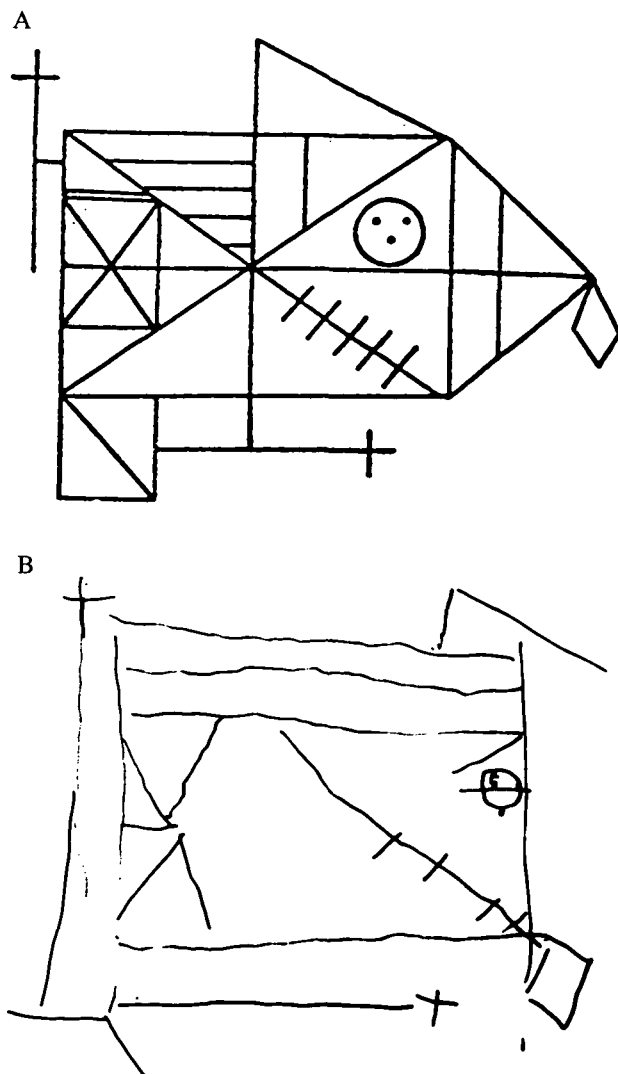


Fig. 7 (A) The Rey-Osterreith Complex figure is depicted. (B) L.M.'s ability to copy this complex geometric figure was severely defective. However, when L.M. engaged in visuo-perceptive tasks that required the recall rather than the reproduction of complex visual patterns, her performance was much improved. L.M.'s copying difficulties could have been related to her previous complaints that she could not track the trajectory of her own right index finger if it moved 'too fast' (see text).

Benton Visual Retention Test

Like the CFT, this test was given with no time restriction. When performance depended upon reproduction by drawing, L.M.'s score was two correct and 20 errors (normal for L.M.'s age is six correct and six errors). This performance was defective (Sivan, 1992). However, when performance depended on recognition rather than reproduction, L.M. again performed much better. The cut-off score for normal performance on VRT versions F and G is 11 out of 15 correct on each version (Benton, 1990). L.M. scored 12 out of 15 correct on version F, and 11 out of 15 correct on version G. In comparison, the scores of two female control subjects (the same tested in 5A) were 13 and 14 out of 15 on F and both 14 out of 15 correct on G. However, here again, L.M. was

slow, requiring 4.4 and 4.5 min, respectively, to perform tasks that took the controls 2.1 and 2.3 min on average to complete.

Hooper Visual Organization Test

L.M. achieved a score of 18 out of 30 with a corrected T-score of 64. While this score indicates a moderate impairment according to the normative data of Hooper (1983), it is proportionally much better than the scores L.M. achieved on the CFT-copy, and BVRT form C.

Mooney's Closure Faces Test

For this task, L.M. achieved 26 correct out of 44. This performance is below expectations for L.M.'s age. As with the HVOT, L.M.'s performance for this task was proportionally much better than the scores she achieved on the CFT-copy, and BVRT form C, and resembled more her performance on the CFT and BVRT matching tasks. In fact, L.M. was able to discriminate difficult items that many normal subjects, (including the readers) have trouble with (see Fig. 8).

Cookie theft picture

L.M. spontaneously reported all the salient features in the display, just as individuals with unimpaired vision and language do. Specifically, she reported 'a scene' of 'a woman washing dishes', and the 'water running over', exactly as depicted on the right side of the display. On the left side of the display she saw 'a girl', and 'a boy reaching and giving something to the girl.' Furthermore, the 'boy is in trouble because he is not allowed in the cookies perhaps' and 'the boy will fall because the chair is falling over.' In short, L.M. had a normal performance on this task.

Discussion of Experiment 4

L.M. was unable to reproduce line drawings of geometrical figures printed at 100% contrast on the BVRT and CFT (see Fig. 7). Such visuoconstructive difficulties are commonly observed in patients with lesions of the posterior right hemisphere. Patient A.F. reported by Vaina *et al.* (1990) is an example (see fig. 2, p. 356, in which A.F. attempts to draw a house to direct copy). These defects are especially marked in individuals with 'visual disorientation' or 'simultanagnosia' due to bilateral lesions of the dorsolateral visual system as reported by Balint (1909).

However, we do not think L.M. has 'visuoconstructive' deficits like those described in right hemisphere cases or in Balint syndrome. Her impaired performances on the CFT and BVRT were evidently task dependent, and not revealing of any inability to perceive or process certain dimensions or features of the high contrast black-and-white static stimulus patterns. Thus, L.M. produced an accurate performance on

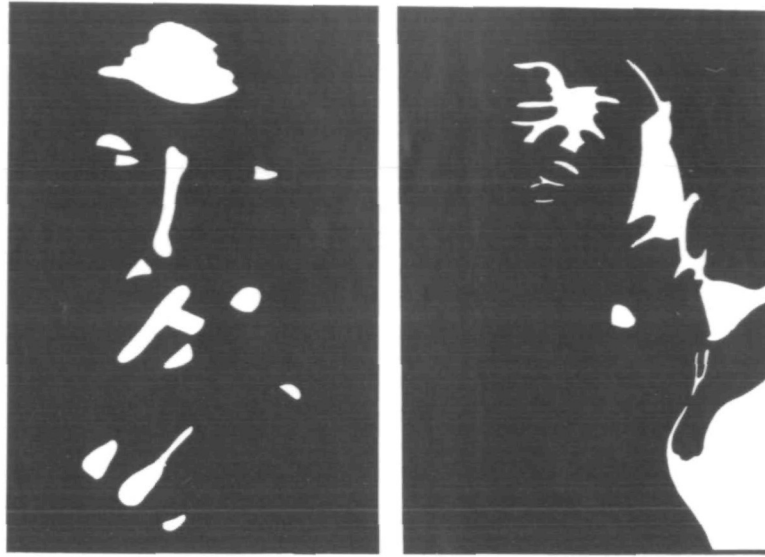


Fig. 8 L.M. can perform sophisticated judgments on complex static stimuli, as long as the stimuli are presented in high contrast, low-noise displays. She correctly judged the age and sex in different black and white incomplete cartoons of faces depicted on the Mooney's Closure Faces test. For example, she correctly identified the figures depicted in plates 29 (*left*) and 44 (*right*), which some normal subjects may even find difficult.

these tasks when the mode of response was changed from reproduction by drawing to forced choice pattern recognition.

Indeed, we find ample evidence that L.M. can perform sophisticated judgments on complex static stimuli, as long as the stimuli are presented in high contrast, low-noise displays, for which her performance on the HVOT, Mooney's Closure Faces Test and cookie theft picture, was evidence. As well, L.M. can still read, i.e. she does not have pure (acquired) alexia. She can recognize objects and faces and thus does not have agnosia, defined in the sense of Milner and Teuber (1968) as a recognition defect in which normal or near normal percepts are stripped of their meanings.

Interestingly the lesions described in Balint's case overlap those described in L.M. [compare the anatomical drawing of Balint (1909) with Zihl *et al.* (1991), fig. 1], and the cases do show some behavioural similarities. Balint's man had optic ataxia, a defect of hand control under visual guidance, and ocular apraxia, an inability to move the eyes to objects of interest. L.M. also had trouble with eye-hand coordination and was unable to track her own finger movements under visual guidance (Zihl *et al.*, 1983). We believe L.M.'s trouble copying patterns such as on the CFT could have been due, in part, to such a deficit. Furthermore, we would not be surprised if Balint's patient also had both a disturbance of smooth pursuit eye movements and of movement perception as L.M. does. Balint did not comment on the former defect, and if he ever considered a movement perception defect in his patient, he probably lacked a means to test it. Descriptions of the phi phenomenon occurred only after Balint's report.

However, judging by her preserved report of the cookie theft picture, L.M. does not have the spatial disorder of attention known as visual disorientation (Holmes, 1918) or simultanagnosia (Wolpert, 1924). Simultanagnosia is the

perceptual underpinning of Balint syndrome and probably represents a variety of combined perceptual defects including VI type scotomata, defective visuoconstructive ability and defective visual attention (Rizzo, 1993). The effect is a marked reduction of the useful field of view. In fact, Balint claimed that his patient could only see one object at a time, no matter what size. Actually, simultanagnosia is not really an agnosia in the sense of Milner and Teuber (1968) and is better covered by the term 'apperceptive agnosia', used by Lissauer (1890). Unlike L.M., simultanagnosics fail to report the major objects and relationships among objects in displays such as the cookie theft. If L.M. has trouble attending to simultaneous stimuli, it is because they are moving (McLeod *et al.*, 1989). In contrast, the deficit described by Balint in his patient and by subsequent authors such as Hecaen and Ajuriaguerra (1954), indicates that the problem perceiving objects in simultanagnosia is more generalized and occurs whether visual targets are moving or are stationary.

Experiment 5: perception of the bistable movement with the Ternus display

The Ternus display (Ternus, 1938) is a two-frame animation sequence depicting movement in a set of three evenly spaced identical bars. Between frames, the set of bars is shifted laterally by one cycle, such that two of the bars lie on the positions occupied by their neighbour in the previous frame (*see* Fig. 9A). A variable length ISI is interposed between the presentation of the two frames. The movement in this display has two possible perceptual interpretations, depending on the ISI duration (*see* Fig. 9B). With long ISIs (100 ms), the set of bars appears to move back and forth *en masse*:

Ternus Display

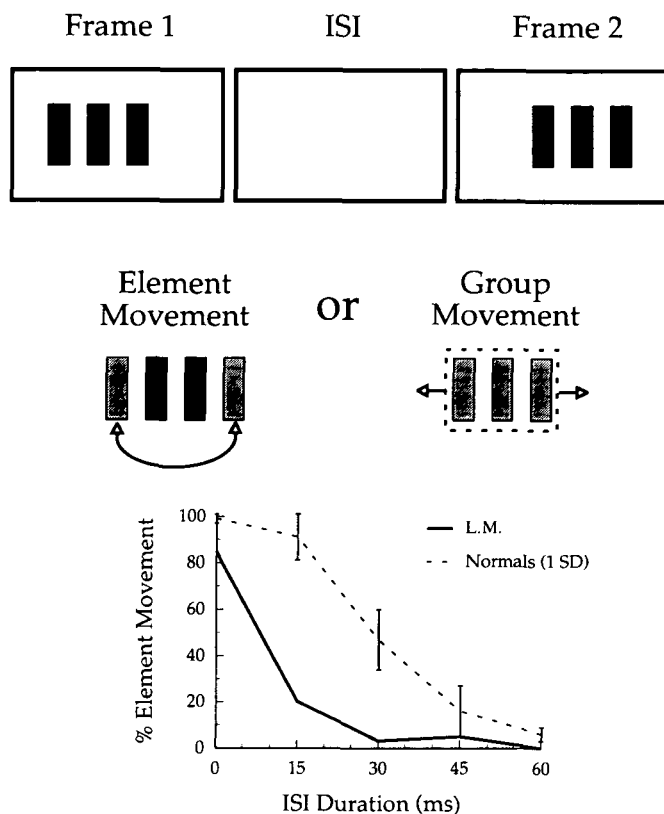


Fig. 9 (A) The three frames of the Ternus display are depicted. Frames 1 and 3 have one element transposed to the opposite end. Frame 2 is a variable ISI during which the screen is blank. (B) With brief ISIs, typically one element appears to move from end to end, termed element movement. With longer ISIs, typically all three elements appear to move together back and forth, termed group movement. (C) The proportion of element movement reports for L.M. and a group of normal observers as a function of ISI duration. Error bars denote 1 SD. L.M. transitioned from element movement to group movement reports at a shorter ISI than normals.

this is called group movement. However, with brief ISIs (10 ms), one bar appears to move back and forth between the two ends, while the middle two bars appear stationary; this is called element movement. The shift from reports of element movement to reports of group movement takes place typically around 40 ms ISI.

These two mutually exclusive percepts are believed to illustrate the dichotomy between the short-range and long-range processes in apparent motion (AM) perception (Braddick, 1980; Petersik, 1989). Pantle and Picciano (1976) suggest that group movement is subserved by the long-range AM process. Both long-range motion and group movement in the Ternus display are perceived under similar conditions. These conditions are: (i) long ISIs; (ii) dichoptic viewing of AM frames; and (iii) contrast reversals between AM frames. Conversely, element movement is thought to be subserved by the short-range AM system, even though element

movement has the longer perceived movement excursion in this display. The short-range system generates the condition for element movement by signalling the 'stationarity' or no movement of the middle two elements (Petersik and Pantle, 1979; Braddick, 1980). As Braddick (1980) points out, 'Any system of directionally selective detectors must have a characteristic null response when no movement occurs.' This null response is responsible for the perception of no movement by the overlapping (middle) elements in the Ternus display. The perceived movement of the outermost element is then likely the product of the long-range system.

The perceptually bistable display described above provides a well-defined paradigm with which to study L.M.'s motion perception. We wondered if L.M. would perceive these two different types of movement with this display, and whether the parameters necessary for seeing each type of movement would be similar to those for normal observers. Not only would this experiment tell us something about L.M.'s perceptual mechanisms, but more generally, L.M.'s performance might provide insight into the different mechanisms underlying the two perceptual interpretations of this display.

Method

The Ternus display used in this study had a three-frame animation sequence depicting three vertical black bars against a white background on the first and third frames (see Fig. 9A). The middle frame was blank, and was presented during the ISI. Each bar was 2.5° tall and $30'$ wide. The bars were interspaced by 1° (two-bar widths). To generate the movement in display, one bar was displaced from one lateral extreme to the other in alternating frames. The interval between frames (ISI) varied as did the frame duration. The ISI was characterized by a solid white background.

Since the display was shown on a 67-Hz monochrome monitor, all stimulus parameters were a function of the 15 ms frame rate. The ISI varied between 0 and 60 ms, in 15 ms intervals. Frame duration was 60, 90, 120 or 150 ms. The selection of these parameters was based on some brief pilot testing. L.M. completed 10 trials for each ISI-frame duration combination for 240 trials in all.

In each trial, the subject viewed 12 cycles of the two frames and the ISIs. The subject's task was to report if the entire set of three figures appeared to move together back-and-forth (group movement), or whether the outside figure jumped from end-to-end. Trials were initiated by the experimenter after signalling for the subject's attention to the screen. The subject's reports were both verbal and gestural.

Results

Since L.M. showed no effect for frame duration the data for ISI across all frame durations is shown in Fig. 9C. For comparison, the performance of six normal observers (mean age 50 years) is shown with error bars denoting 1 SD. The performance of our normal observers is similar to that

previously reported by Pantle and Picciano (1976) and Petersik and Pantle (1979) with a 200 ms frame duration.

L.M.'s performance was broadly similar to that of normal controls. She reported a greater proportion of element movement with shorter ISI and more group movement with longer ISI. Also, like normal controls, L.M. continued to report group movement with longer ISIs. However, there was an important difference in L.M.'s performance. In particular, the transition in reports of element to group movement occurred at a very short ISI. In fact, L.M.'s reports were predominantly of group movement at ISI of only 15 ms. The transition in normals occurs between 30 ms ISI (the current study) and 40 ms ISI (Pantle and Picciano, 1976).

Discussion of Experiment 5

L.M.'s phenomenal reports of the stimulus movement are interesting. She reported no perception of element movement in these displays with brief ISIs. Instead, L.M. described that the outer element appeared to 'blink' on and off, on opposite sides of the middle overlapping elements. She perceived no movement of this element between the two ends. This coincides with her reported loss of long-range movement perception (Hess *et al.*, 1989). Her phenomenal descriptions in conditions of group movement were similar. With the longest ISIs, L.M. reported that the group of elements appeared mostly to 'flash' at the two locations without a percept of movement between them. With shorter ISIs, L.M. tentatively reported some movement of the group of elements between the two locations, similar to that which normal observers would report. This suggests that L.M. may have some ability to see some long-range movement or that these limited reports of movement were mediated by a short-range mechanism. Regardless of what limited motion perception remains, it is apparent from L.M.'s ease in performing the task that she could infer movement from the 'flashing' or 'blinking' of the stimulus elements even if she did not perceive actual movement.

One alternative explanation for L.M.'s performance is that L.M. simply detected flashing in the middle overlapping elements and gave an appropriate response. This simple strategy is possible even though the subject did not know the purpose of the test and the 'normal' pattern of results; i.e. when the middle elements appear to flash (a long ISI), the more appropriate response is 'group movement'. However, when the middle elements do not appear to flash (a short ISI), the more appropriate response is element movement. By detecting flashing, a subject could produce a ISI dependent change in reports of element and group movement.

However, this pattern of responding is unlikely to generate the results shown for L.M. in Fig. 6. She demonstrates normal flicker fusion frequency of ~30 Hz. This means stimuli at 15 ms ISI should appear almost continuous (i.e. not flash), especially with these comparatively long frame rates of 60–150 ms. Therefore, L.M. was not simply detecting and

reporting on stimulus flashing. If she had been, her transition from reports of element movement to reports of group movement would have been at a longer ISI, and appeared more similar to normal observers. On the contrary, another alternative explanation is that L.M. has unusually brief visual pattern persistence which might not have been detected upon testing her flicker fusion frequency. Breitmeyer and Ritter (1986) found that increased pattern persistence extends reports of element motion to longer ISI durations, supposedly by contributing to the temporal integration of pattern and to the perceptual stationarity of the two inside elements. As L.M. transitioned to reports of group movement at a very brief ISI, it remains a possibility that she exhibits very short pattern persistence, the reverse of Breitmeyer and Ritter's finding. Inasmuch as visual persistence contributes to temporal integration of pattern (Di Lollo and Woods, 1981), it is important to consider that such a deficit might interfere with the integration of local dots movements in to a percept of global flow in the RDC used to assess motion perception. This possibility was not pursued in this set of experiments.

We believe the pattern in which L.M. reported group or element movement supports the notion of Hess *et al.* (1989) that motion perception in L.M. depends primarily on residual short-range processes. Long-range motion processing appears to be limited, and L.M. does not even report seeing phi-movement (Zihl *et al.*, 1983). With the Ternus display, it appears that L.M.'s short-range system operates at 0 and 15 ms ISI to signal the stationarity of the overlapping elements. By 30 ms ISI, L.M. reports only group movement, whereas normal subjects still report element movement on half the trials. This difference may result from the limited nature of L.M.'s residual short-range motion processing, which fails to detect whether the overlapping elements are stationary at longer ISI. In such cases, L.M. reports group movement.

The results of this experiment suggest that actual perception of both element and group movement in the Ternus display is mediated by the long-range motion system. For the most part, L.M. saw neither. However, the difference between the two percepts might be based on the activity of the short-range system as previously proposed. When L.M.'s limited short-range system was presented with an appropriate spatio-temporal stimulus, it actively signalled a null response. A longer ISI made it an ineffective stimulus, L.M.'s short-range system did not signal 'stationarity', and therefore group movement was reported.

Conclusion

Summary

L.M. has a severe, persistent defect of motion perception. While L.M. can still perceive a directional motion signal, the results in Experiment 1 indicate this ability is highly sensitive to noise, as first indicated by Baker *et al.* (1991). Similarly, L.M. can perceive 2-D shape and 3-D SFM, but

Table 2 *Magnitude of perceptual deficits measured in subject L.M.*

Perceptual function	Deficit magnitude
Global coherent motion direction discrimination	Severe—at moderate noise levels
Perception of 3-D structure	
from motion	Severe—even at 100% signal
from dynamic stereopsis	Severe—at moderate noise levels
Perception of 2-D shape	
from motion cues	Severe—at low noise levels
from transient ('on' and 'off') cues	Severe—at low noise levels
from static texture cues	Severe—for certain textures
	Minimal—for dot density cues
from static stereo cues	Severe—even at 100% signal
from dynamic stereo cues	Severe—even at 100% signal
'Visuoconstructive' abilities	
for 2-D stimulus presented at maximum contrast	None to moderate—as long as drawing not required
Apparent (ϕ) movement in Ternus display	Mild to moderate at short ISI and severe at long ISI—suggesting absent 'long range' mechanisms

even moderate levels of noise causes a breakdown in these abilities (Experiments 2 and 3). L.M.'s perceptual reports in viewing the Ternus display (Experiment 5) were similar to normal, however, it appears that L.M. does not perceive long-range motion. Moreover, L.M.'s perceptual deficits extend outside the processing of motion (Experiments 3 and 4). L.M. also has marked difficulty perceiving 2-D shapes defined by non-motion signals including 'transient' on-off cues, dynamic and static stereo cues, and different static textures (see Table 2).

Akinetopsia and area MT (V5)

The pattern of perceptual deficits in akinetopsic subject L.M. does not resemble the pattern of M-pathway, P-pathway, or area V4-type dysfunction observed in monkeys (Schiller and Logothetis, 1990; Schiller, 1993). Baker *et al.* (1991) likened L.M.'s poor CS for the direction of drifting sine wave grating and decreased direction discrimination of RDC to the pattern in animals lacking direction sensitive neurons in visual cortex due to rearing under stroboscopic light. More recently, Plant and Nakayama (1993) compared L.M.'s underestimation of target speed to the errors reported by Newsome *et al.* (1985) in monkeys with area MT (V5) lesions. Perhaps so, but the perceptual profiles measured in this study indicate that the pattern of perceptual deficits in L.M. extends beyond motion processing and area MT (V5) dysfunction.

Another distinction between L.M.'s deficits and simian area MT (V5) dysfunction concerns the longevity of the deficits: L.M.'s motion trouble has persisted for over a decade, whereas area MT (V5) dysfunction in monkey recovers rapidly. A likely reason is that area MT (V5) dysfunction is created by making millimetre-sized chemical lesions in simian cortex using ibotenic acid (Newsome *et al.*, 1985), which largely spares the white matter. On the other

hand, L.M.'s deficits are caused by cerebrovascular lesions which are larger and more destructive. They are bilateral, and widely surround the location of a putative human MT area (V5) homologue as depicted in a PET study by Watson *et al.* (1993). Due to their extent, the dorsolateral lesions in L.M. may also include homologues of simian middle superior temporal area, floor of the superior temporal sulcus and lateral intraparietal area (Ungerleider and Desimone, 1986; Boussaoud *et al.*, 1990; Tanaka *et al.*, 1993) which also process motion, and affect the white matter connections underlying these regions. Interestingly, Pasternak and Merigan (1994) reported that simian MT area lesions produce deficits that are graded in relation to lesion extent.

Residual movement perception

Despite extensive and critically located lesions in the dorsolateral visual pathways, L.M. is not fully motion blind. This observation is compatible with the idea that the representation of motion in the primate visual system is redundant (Ferrera *et al.*, 1994). A human homologue of the monkey's area MT (V5) complex may play an important role in motion processing, but it does not operate in isolation. Rather, it should function in concert with other structures in a network for human motion perception, including the superior colliculus, frontal eye fields, parieto-occipital cortex, dorsolateral pontine nucleus, and even the cerebellum (Nawrot and Rizzo, 1995). Residual motion processing in L.M. might also depend on portions of the cuneus, precuneus (Shipp *et al.*, 1994), and ventromesially located structures such as the fusiform and lingual gyri, which were spared in L.M. The latter regions are thought to contain a human area V4 homologue (Zeki, 1990), and the evidence in monkeys indicates V4 possesses a rudimentary motion processing

capacity (Schiller, 1993). Based on Experiment 5, such a residual capacity includes a combination of short-range and defective long-range apparent motion mechanisms. Of course, L.M. can always infer motion by making use of any available information on object displacements, but this is not true motion perception.

Two visual systems

The hypothesis of 'two visual systems' in primates suggests a 'what' pathway for perceiving and recognizing objects, and a 'where' pathway for locating those objects in space (Ungerleider and Mishkin, 1982; Damasio, 1985). In the human brain, such pathways are thought to segregate along a ventromesial to dorsolateral axis (Rizzo, 1994). The dorsolateral pathway begins above the calcarine fissure in occipital areas 18 and 19 and extends into adjacent parietal and temporo-parieto-occipital regions located on the lateral surface of the brain. These regions include areas 5, 7, 39, 37 and superior 19, portions of which were damaged in akinetopsic subject L.M. A ventromesial visual pathway begins in the human occipital lobe beneath the calcarine fissure, connects with adjacent temporal regions, and may include human homologues of the monkeys' areas V4 and IT. L.M. has no evidence of damage to these latter structures, yet she can be construed to have a 'what' deficit based on her trouble perceiving 2-D shapes and 3-D objects defined by a variety of different, motion and non-motion cues. These findings indicate that the ability to segregate figure-from-ground is not a unique property of the ventromesial visual association areas. Rather, the dorsolateral association areas, which should contain a human homologue of simian area MT (V5), are also capable of making a significant contribution to this process, especially when dynamic cues are involved. The notion that the processing of information on textures, patterns, shapes and objects depends exclusively on a ventromesial or 'what' pathway in the human brain is an oversimplification because parallel pathways have cross-talk and converge (Martin, 1992; Merigan and Maunsell, 1993).

The role of visual association cortex in extracting signal-from-noise

As mentioned, the motion direction discrimination in L.M. is critically sensitive to noise, both moving and stationary, a result in clear agreement with Baker *et al.* (1991). Interestingly, so is the perception of 2-D shape and 3-D SFM. The last result resembles the finding in motion deficient patient A.F. reported by Vaina *et al.* (1990) who had trouble perceiving 3-D SFM at lower motion signal to noise ratios. Together these findings highlight the role of visual association cortex, including a possible homologue of the monkey's area MT (V5) complex and connections, in 'sharpening' our picture of the world and thereby increasing the accuracy of our perceptual judgments and decisions (Salzman and Newsome, 1994). This function is accomplished by reducing

the effects of stationary and motion noise which is ever present in the visual scene, inherent in the operations of visual neurons, and also caused by the ceaseless jitter of any normal observer's eyes. The latter role would depend on efference copy, the monitoring of corollary discharge from eye movements, perhaps in connection with the cerebellum. The cerebellum plays a role in motion perception (Nawrot and Rizzo, 1995) and motor control including eye movements, contains cells in its vermis which are sensitive to the direction of movement of visual targets resembling those in area MT (V5), and forms part of a CNS network that includes MT area (V5). Interestingly, the most recent anatomical studies of L.M. both show a significant midline cerebellar lesion (Zihl *et al.*, 1991; Shipp *et al.*, 1994).

Acknowledgements

This work was supported by NIH PO NS19632, McDonnell-Pew Program in Cognitive Neuroscience, and MRC Canada.

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Received December 8, 1994. Revised April 3, 1995.

Accepted April 14, 1995