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Selective Impairment of Visual Motion Interpretation Following Lesions of the Right Occipito-Parietal Area in Humans

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Abstract. A group of eighteen patients selected on the basis of the anatomical locus of the lesion, normal visual acuity and the ability to discriminate visual motion, were assessed on the perception of Julesz Random-Dot stereograms and on three tasks of visual motion interpretation: Speed Discrimination, 3D-Structure-from-Motion and 2D-Form-from-motion. The results on these experimental tasks demonstrate a double dissociation of deficits on the visual analysis of motion and stereopsis in the patients with lesions to the posterior right hemisphere. The right occipital-parietal (ROP) group failed on the Stereopsis task and showed a dramatic impairment on the Speed Comparison and on the Structure-from-Motion experiments. They performed in the normal range, however, on the 2D-Form-from-Motion task. The right occipital-temporal (ROT) group, on the other hand, were severely impaired on the identification of two dimensional forms from motion or stereopsis. In both cases, however, they were able to obtain a coarse segregation of the figure from the background. The ROT group did not present significant deficits on the Speed Discrimination and the Structure-from-Motion tasks. The results are discussed in the light of recent physiological and psychophysical findings, and it is hypothesized that, in the human brain, visual deficits of *motion interpretation* and of *stereopsis* are associated with right occipital-parietal lesions.

1 Introduction

Motion pervades the visual world, and the human visual system uses it in several ways, to carve the scene into separate objects and to break camouflage (Koffka 1935; Julesz 1971), to control eye movements which allow the observer to track objects of interest, and to recover three-dimensional structure (Wallach and O'Connell 1953; Ullman 1979).

These are fundamental abilities of the visual system and they seem so direct and effortless, that naturally, one is inclined to take them for granted. Only after losing the ability to perceive movement is it obvious how extraordinarily dependent we are on it for coping with the demands of the everyday life. Several cases of patients suffering from a specific disorder of movement perception (Goldstein and Gelb 1918; Potzl and Redlich 1911; Riddoch 1917) have been documented in the neurological literature. The anatomical data converges to indicate that bilateral damage to areas in the posterior brain may account for this deficit. The most eloquent example is a recent detailed case report (Zihl et al. 1983) of a patient, L.M. with a bilateral occipital-parietal lesion. Her main deficit was the nearly complete inability to perceive movement. Moving objects were seen as present in one location and then in another, but with little or no intervening movement. She had severe difficulties in coping with the real world; thus crossing the street in the face of on coming traffic was difficult because a car would seem far away and then suddenly it would be dangerously close, or she was unable to pour a cup of coffee without the risk of having it overflow.

On formal testing, L.M. had intact visual fields, normal visual acuity, stereopsis, colour perception and form discrimination. However, she revealed a selective disorder of movement perception and she lacked pursuit eye-movements although the saccadic eye-movements were preserved.

Such dramatic impairment of movement detection adds substantial evidence to the view that movement vision forms a separate system. In the initial stages, motion processing apparently operates in parallel with other early processing modules specialized for extracting sensory information about color, depth, form or spatial localization, for example. But beyond the initial detection stage, the analysis of visual motion may be carried out by several distinct subprocesses which solve different motion problems and which are supported by different visual structures (for a review see Nakayama 1985; Hildreth and Koch 1986).

The variety of motion tasks carried out in the human visual system may be conveniently grouped into two classes: *tasks of separation* and *tasks of integration* (Marr and Ullman 1981). Separation tasks are those that involve instantaneous and local measurements of velocity, which are useful for separating figure from the background and which operate over short spatial and temporal ranges (Braddick 1974, 1980). Tasks of integration, on the other hand, are higher level processes which involve more complex motion information resulting from the combination of simpler motion measurements, presumably integrating information that is extended in time and space. Thus, Adelson and Movshon (1982) in an interesting psychophysical experiment have shown that the motion of a complex plaid pattern (created by the superimposition of two sinusoidal gratings each moving in a direction orthogonal to its orientation) is perceived by human observers as moving in a direction that is different from that of either component. This result suggests that at some level of processing, the brain integrates the motion of the components into the motion of the resulting pattern. Another example, of a different nature, is based on Ullman's (1979) computational theory for the interpretation of visual motion. This suggests that for the recovery of three dimensional structure from motion, the local information about the velocity values would be insufficient. Instead, this task requires integration of information from two or more motion frames.

The purpose of this investigation is to study whether patients with posterior brain lesions whose ability to discriminate motion is preserved, may present deficits in other aspects of visual motion analysis. Specifically, the current anatomical and physiological data from studies of subhuman primates support the existence of a motion pathway that originates in striate cortex and terminates in higher cortical areas of the posterior parietal lobe (Maunsell and Newsome 1987). Could one find as specific a correlation between particular aspects of motion processing and neural mechanisms in man, as it has been demonstrated in subhuman primates?

The question of specialization of areas in the posterior brain in humans for different aspects of motion processing has motivated us to develop an extensive series of motion experiments (Vaina et al. 1987). In three of these experiments we studied the performance of a group of stroke patients with posterior unilateral lesions involving tissue in the occipital, temporal and parietal lobes. In all cases, the primary visual cortex was spared. We studied the performance on tasks involving the identification of the 2D-form-from-motion, speed of motion, and the recovery of structure-from-motion. The 2D-form-from-motion experiment involves the recognition of two dimensional shapes from random dot kinematograms. This experiment is viewed as a task of first *separating* a figure from the background by motion cues, and then *recognizing* the shape of the figure. The last two experiments are viewed as tasks of *integration* of various local motion measurements.

The basic a priori hypothesis of this study is that, in humans, right occipito-parietal lesions are associated with deficits of visual motion analysis, specifically, with tasks of motion integration (Vaina 1988a, b, Vaina et al. 1988).

2 Methods

2.1 Subjects

Eighteen patients and six control subjects participated in this study. All the subjects were right handed. Each patient had undergone a unilateral stroke limited to the posterior brain involving tissue in the occipital, parietal or temporal areas. On the basis of radiological information the patients were classified according to the side and specific site of lesion into the following groups: left (8 subjects)[1], and right (10 subjects). The right hemisphere group (subjects 1–10 in Table 1) was subdivided further into occipital-temporal (5 subjects) and occipital-parietal subgroups (5 subjects). The lesion localization was done by a neuroradiologist on the basis of the CT scans interpreted according to a cranial computed tomography atlas (Kretschmann and Weinrich 1986). This atlas presents the main pathways of the neurofunctional system using the CT planes, and illustrates the cerebral vessels and their territories according to their clinical relevance.

The patients (except E.S.) were selected from the inpatient population of the Young Stroke Unit of the New England Rehabilitation Hospital. They were hospitalized for rehabilitation of physical, cognitive or speech functions, and at the moment of testing they were between 6 and 9 weeks post stroke. The summary of the neurological, neuropsychological examinations and the neuroradiological localization of lesion by CT scan is presented in Table 1.

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[1] The lesions in the left hemisphere group subjects were somewhat less well defined and not always comparable to the lesions of the right hemisphere group. In several instances the left hemisphere lesions resulted from CVA involving the posterior branches of the Middle Cerebral Artery. The lesions of the right hemisphere group were entirely caused by the CVA involving the Posterior Cerebral Artery

Table 1. Summary of the neurological, neuropsychological and demographic characteristics of the patients included in the study. The following abreviations were used: R-OT and R-OP for right occipital-temporal and right occipital-parietal respectively; VFD = visual field deficits. Coloumns 6–12 show the results on the following subcomponents of the Wechsler Adult Intelligence Scale-Revisted: VIQ = Verbal IQ, MIQ = Memory IQ; PIQ = Performance IQ. BD (Block design), OA (Object assembly) and PA (Picture arrangement) are subtests of the Performance IQ battery. By "–" we noted that the information was not available

Patient No.	Age	Sex	Site of lesion	VFD	IQ	PIQ	VIQ	MIQ	BD	OA	PA	Stereo
1	60	F	R-OT	L	–	68	–	101	2	2	4	Impaired
2	37	M	R-OT	L	87	84	84	94	99	8	8	Impaired
3	49	F	R-OT	L	–	–	115	93	7	3	6	Impaired
4	61	M	R-OT	L	–	–	105	100	6	5	7	Impaired
5	28	F	R-OT	No	68	66	71	–	4	4	5	Impaired
6	44	M	R-PP	L	90	73	107	129	5	5	5	Absent
7	47	M	R-OP	L	99	84	113	143	6	8	8	Absent
8	52	M	R-OP	L	83	79	87	100	6	7	5	Absent
9	40	M	R-OP	No	99	93	97	104	9	10	12	Absent
10	60	F	R-OP	L	–	–	107	–	7	3	4	Absent
11	59	F	L-P	No	76	73	81	57	3	3	2	Impaired
12	59	M	L-OP	R	–	72	–	–	5	8	8	Good
13	67	M	L-OT	No	–	–	–	–	7	3	4	Good
14	39	M	L-OT	No	–	72	–	–	4	7	7	–
15	67	M	L-T	No	75	81	73	57	4	5	14	Good
16	58	F	L-OP	R	–	–		–	7	7	8	Good
17	69	F	L-P	No	102	102	100	108	11	13	11	–
18	69	M	L-OP	R	–	87	–	103	7	7	8	Impaired

None of the patients included in the study had double vision, significant eye movement disorders[2] or a significant reduction in visual acuity for near vision to an extent that would interfere with the reliability of test results. All the subjects[3] had normal depth vision prior to the stroke (they reported that they have seen and enjoyed "three dimensional movies").

The subjects in the left hemisphere patient group (the subjects 11–18 in Table 1) usually had aphasia, but only those patients were included in the study who were able to understand the task and could submit to formal testing. There was no known history of alcohol or drug abuse, psychiatric or seizure disorder in any of the subjects participating in the study. The six control subjects were selected to match the patient group as closely as possible with respect to age, sex, handedness, educational level and socio-economic status. The control subjects did not undergo standard neuropsychological tests.

2.2 Neuropsychological Investigations

As part of the routine neuropsychological evaluation the patients included in the study were tested on subtests of the Wechsler Adult Intelligence Scale Revisted (WAIS-R) and their Verbal IQ, Memory IQ and Performance IQ's are given in Table 1.

All the patients had been given three components of the following subtests of the Performance IQ: Block Design (BD), Picture Arrangement (PA) and Object Assembly (OA). The analysis of the performance of a large group of brain damaged patients ($n = 656$) on the different subtests of the WAIS-R, indicated that the right occipito-parietal group ($n = 22$) showed a clear-cut laterality effect, with the right hemisphere occipito-parietal group being more impaired on the above subtests of the Performance IQ battery than the corresponding left hemisphere ($p < 0.01$) group (Warrington et al. 1986). Also the right parietal group was more impaired on these tasks than the right non-parietal group.

The results of these tests for our groups of patients showed that they are strongly correlated among themselves ($r = 0.40$ to 0.67). As the Block Design, Picture Arrangement and Picture Completion tests are related subcomponents of the Performance IQ component of the WAIS-R, their results could be combined, thus creating a more stable and reliable variable (their sum) for further comparison with the experimental motion tasks. This also eliminates potential problems

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[2] Defective eye movements as an explanation of the impairment on these tasks in the occipito-parietal group is a priori excluded. Although the parietal-occipital junction controls ipsilateral smooth pursuit (Bajandas and Kline 1987), this is necessary for tracking of moving objects, but eye movements are generally not accurate enough for encoding the exact magnitude of speed or velocity of motion (McKee 1981; Nakayama, personal communication)

[3] One subject in the Right Occipito-Temporal group was 28 years old and she said that "those movies were before her time"

with significance levels that would occur if multiple testing were done with 3 correlated variables. Hence, the cumulative results on these three tests will be further correlated with the experimental tasks.

2.3 Experimental Tasks

The testing sessions lasted 45 min, and were carried out at the New England Rehabilitation Hospital. All the patients were first assessed on a task of stereoscopic vision with a subset of random dot stereograms devised by Julesz (1971).

All the other experimental tasks were carried out under the control of a computer (Apple 2E with 64 K of memory) which displayed the targets, compiled, analysed and saved the responses and printed out the results as number of correct responses and mean reaction times. The display was a 12 inch black-and-white monitor subtending 20° by 15° of visual angle with a resolution of 280 by 192 pixels. Only one intensity level is used. The screen was "refreshed" 30 times per second. The responses were recorded by pressing specially designated keys on the computer keyboard.

The viewing distance was kept constant at 65 cm and at this distance each pixel subtended 5×4.3 arcmin. The rate of presentation of the stimuli was roughly 12 trials per minute, except for the *structure-from-motion* task which had only one trial. All stimuli were viewed binocularly under a condition of free eye movements. The position of the display was arranged so as not to interfere with the area of visual deficit and the stimuli were displayed only in central vision.

Prior to administering each test the subject was trained on a series of examples (3 trials) to became familiar with the computer display and with the specific task. All the tests were administered by the same examiner and in the same room with a constant low-level ambient illumination.

2.4 Statistical Analysis of the Data

The analysis of the data was done using the SAS statistical package on an IBM PC. Preliminary analyses of the data distribution for the motion tests indicated that the variance differed greatly among subgroups and were resistant to stabilization with transformations (arcsin and log transformations). Since the subgroups were generally small and variable in size, nonparametric tests were most appropriate. The fundamental hypothesis of this study is that the patient group with right occipito-temporal lesions, and the patient group with lesions to the right occipito-parietal area, will perform differently on the tasks addressed here. Thus they were considered as two different groups from the beginning. No further breakdown was carried out in the left hemisphere brain damaged group, the subgroups were too small for any statistical analysis. The reaction time data was not used as a parameter for the comparison of the different patient groups on the visual tasks. The main reason for this was that reaction time does not separate the motor and the sensory component of a task. Another reason was that reaction time data and neurophysiological data cannot be directly compared.

The overall comparison of the patients' performance was carried out by performing a Kruskall-Wallis test on the Normal vs LBD vs ROP vs ROT subject groups with a significance level of $\alpha=0.05$, followed by selected Wilcoxon paired tests with the Bonferroni adjustment to significance level (alpha/number of tests) to protect against false positives.

3 The Stereopsis Task

3.1 Form from Stereopsis (Julesz' Random Dot Stereograms)

An object in the world projects two slightly different images on the retinae of the left and right eyes, and binocular stereopsis is the process that recovers the description of 3D structure from these different images. In the random dot stereograms presented here, there is no information about the visible surfaces except through stereo disparity. Julesz (1971) demonstrated conclusively that binocular combination occurs quite early in visual processing, at a level prior to object recognition. The stereopsis problem is characteristically regarded as consisting of two subproblems: (*1*) the *correspondence* problem (Julesz 1971), which is the problem of measuring the pattern of disparity between the two images, and (*2*) the *interpretation* problem, which is the use of disparity information to recover the orientation and the distance of surfaces in the scene.

The patients were tested with a series of random-dot stereograms from the series devised by Julesz (1971). When these targets are viewed monocularly each appears as a random array of small light and dark squares in which no form or depth is apparent. The two random not patterns are identical except that in one pattern the dots in the central region have been displaced laterally with respect to the same region in the other pattern. There are no monocular cues to depth in these patterns but with binocular fusion a central figure stands out in front of the surround.

As in Julesz (1971) the patterns were printed in pale red and green ink. When viewed with a green filter over one eye and a red filter over the other, the central figure is seen in front of (or behind) the surround.

The test consisted of 5 random-dot stereograms. The subject's first task was to say whether he saw a central figure standing away from the surround, and the second task was to identify the shape of the figure.

All the figures were simple geometric forms. If the subject was unable to identify the forms verbally, he was shown the silhouette of four possible matching choices, and was asked to choose which of the silhouettes corresponded to the the figure presented stereoscopically.

3.2 Results and Discussion

The left hemisphere group was able to see the figure in the random dot stereograms. The right hemisphere group, on the other hand, was quite impaired and showed an interesting pattern of deficits. Patients with occipito-temporal lesions, (cases 1–5 in Table 1) were usually able to detect that there was something in the random dot pattern (they could point to it) but they were unable to identify the form or to follow the contour. Asked to describe what they saw in the image, these subjects usually said that "there is something right there", but they did not know what shape it was. Case 3 described seeing figures of real objects (e.g. rabbit, flower). Case 1 had no impression of seeing any figure, she saw only dots.

The right occipito-parietal group (cases 6–10 in Table 1) failed totally on this task. They reported seeing just dots, and "nothing else". Cueing by indicating the areas in the pictures covered by the figure did not help.

These results are interesting for two reasons. First, the fact that the left hemisphere brain damage group presented with no difficulty on this task confirms the view of the right hemisphere superiority for stereopsis (Benton and Hecaen 1970). Second, although both subgroups of right hemisphere subjects (the ROP and ROT) presented with impaired stereoscopic vision, the quality of their deficit was fundamentally different. Thus, while none of the five subjects in the ROP group was able to see anything at all in the random dot stereograms, the subjects included in the ROT group reported an impression of "seeing something", but they failed to identify the shape. This suggests that, at least to a certain extent, the subjects with ROT lesions were able to achieve *correspondence*, at least at a coarse level. Their inability to extract form may be accounted for by a failure to compute correspondence at finer levels, by failure to integrate local information about disparity boundaries into a coherent object outline or form, or by an inability to carry out the coarse-fine integration (Vaina 1987a) necessary for *interpreting* the disparity information to recover exact form.

The right occipito-parietal group completely failed on the stereopsis task, suggesting an inability to achieve *correspondence*. A possible explanation for these results would be a lack of vergence eye movements. Clinically, the vergence deficit has been associated with the occipital-mesencephalic pathway (Bajandas and Kline 1987). One role of vergence eye movements is to eliminate small vertical disparities, and to bring the two images in register. Nielsen and Poggio (1983) showed that for random dot patterns, a registration process based on eye movements must precede the stereomatching process to remove vertical disparities larger than about 4′–7′ which is in the range of the disparities used in the stereopsis task.

4 Visual Motion Analysis Tasks

Three visual motion tests were administered to each subject: *2D-Form-from-Motion, Speed Discrimination and Structure-from-Motion.* The results on these three tasks for the three patient groups and the normal controls group are presented in Table 2.

4.1.1 2D-Form-from-Motion (Random Dot Kinematograms). This experiment addresses two tasks. The first task is figure and ground separation through motion. The second, is the identification of the exact form in clusters of adjacent dots translated across a random dot static display. Psychophysical studies have shown that clusters of dots sharing some common properties are the basis for object separation, and one of the most important properties underlying the grouping of dots is movement of the same velocity and orientation (Julesz 1971).

The whole display is filled with a stationary fine-grained random pattern (50% white and 50% black dots). Each dot subtends 4.33 min × 4.97 min of visual arc. The sensation of two moving textured planar surfaces is elicited by two "random dot kinematograms" defined as two patches of contiguous random dots uniformly displaced from one frame to the next in translational motion across the display. The shapes of the moving patches were selected from the following choices: square, circle, flower, cross, heart and triangle. The patches were shifted by 8.7 arcmin in each successive frame, giving the impression of two forms segregated from the surround translated across the static random-dot display. The interstimulus interval between two consecutive frames was approximatively 70 ms. The form was defined completely by the relationship of the displacement between two patterns.

One figure is translated from left to right and the other from right to left (Fig. 1a). Each cluster of dots subtended an area of about 2.2° × 2.2° of visual angle and the actual speed of the displacement was 1.3°/s.

The two clusters of dots were moved using a commercially available graphics package for the Apple II, the Graphics Magician (Jochumson et al. 1983).

The subject's task was to first discriminate the two moving patches from the static random-dot background, and second, to determine whether they had the

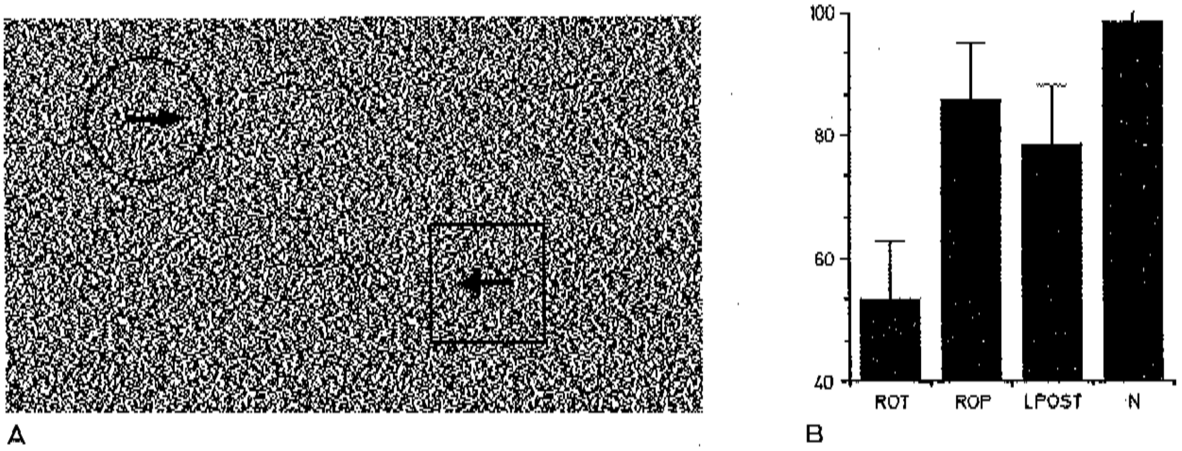

Fig. 1A and B. 2D-Form-from-motion task. **A** The display consisted of a fine grained static random dot pattern resulting from 50% black and 50% white dots. Two patches of contiguous dots were coherently translated across the screen with equal speeds. The task was to determine whether the two translating 2D-shapes were the same or different. The shapes were chosen from the following choices: triangle, square, cross, circle, oblong vertically or horizontally oriented; **B** The percentage of correct responses as function correct matches of the moving shapes. The mean percentage correct responses of the four subject groups are the following: (*a*) normal controls: 98.3%; (*b*) left posteriors: 78.6%; (*c*) right occipital-parietal: 85.5%; (*d*) right occipital-temporal: 53.7%

same shape or not. There were 30 trials and for both subtasks the answers were scored right and wrong for calculating percentages correct. Chance was considered at 50% correct response.

4.1.2 Results and Discussion. The moving clusters of dots were perceived effortlessly by all subjects as two figures clearly segregated from the stationary background. However, there was a significant difference between the ROP and ROT patient subgroups in the ability to identify the shapes (same or different) of the two moving patterns.

To address the relevance of this difference, a Kruskal-Wallis statistical test was used over the individual subject means in the four subject groups: *1*) the normal controls, *2*) left hemisphere brain damaged group, and *3*) the ROP and *4*) the ROT brain-damaged groups. The results indicate that the four groups were different at a significance level of $p < 0.0011$ ($\chi^2 = 16.08$ and $Df = 3$). The ROP and the ROT groups differed significantly by the Wilcoxon's test ($Z = 2.09$, $p < 0.037$), with the ROT's being more impaired (Fig. 1b). The ROP group did not differ significantly from the left hemisphere brain damaged group.

There was no statistical difference between the normal controls, the left hemisphere and the right occipito-parietal groups in the ability to identify whether the moving patterns had the same shape. The right occipito-temporal group, however, was severely impaired on this task. As in their responses to the stereopsis task, they were able to *detect* the (moving) patches, but they consistently failed to identify the specific *form* of the patches.

Thus the right occipito-temporal brain-damaged group was able to perceive the coarse form (the general area) on the basis of motion and stereopsis, but in both cases they failed on the task of identifying their specific form. These results are consistent with a coarse to fine strategy of processing. Such a strategy is computationally useful because there are fewer features at larger scales and therefore there is less ambiguity facing the tasks of integration (Vaina 1987a, b). Another possibility is that the subjects with right occipital-temporal lesions were unable to integrate the coherent boundary of the figure from the local measurements.

4.2.1 Speed Discrimination. Speed refers to the rate of motion and its value is equal and constant for each of the moving dots displayed within one square. The display presents dots moving in random, brownian-like motion, and thus the overall direction of the movement does not play a role in this experiment. However, each individual dot is characterized by a local direction and speed which are described by a local velocity vector. The magnitude component of these velocity vectors is identical for all the dots of one square and forms the basis for a grouping into a global, coherent "speed field".

The Speed Discrimination task tests the ability to measure the speed of movement and to obtain and compare "speed fields". Two squares, 6.7° × 6.7° each, are displayed simultaneously, side by side, on the screen (Fig. 2a). The distance of the center of the squares from the fixation point is 6.3°. In each square 12 small white square dots, each subtending an area equal to 21 min × 21 min of visual angle, were moving

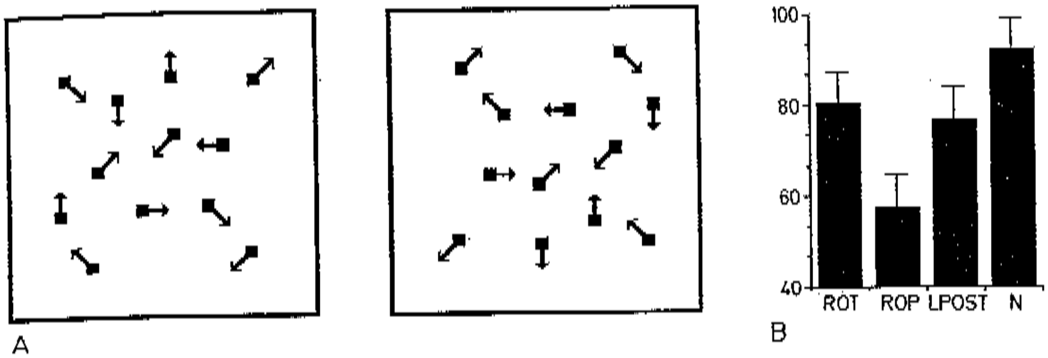

Fig. 2A and B. Speed discrimination task. **A** The display consisted of two squares of dots moving in randomly distributed directions. In each square, for a given trial, the speed of all the dots was constant forming the basis for grouping into a global, coherent, speed field. The task was to determine whether the speed in the two squares were equal. **B** Percentage of correct responses in the speed-discrimination task. The mean percentage correct responses of the four subject groups are the following: (a) normal controls: 90.0%; (b) left posteriors: 76.9%; (c) right occipital-parietal: 57.8%; (d) right occipital-temporal: 80.3%

(bouncing) in random directions. The dots are perceived to move in random directions ("swarm of bees"). The speed of the movement is manipulated by varying the distance (dx) between dots (that is the number of pixels between frames) while keeping the number of frames constant (16 frames/s).

Each dot survives for approximately 60 ms before it vanishes and is replaced by a new dot at a randomly selected location within the square at a distance varying between 1 and 4 pixels (approximatively 4.3 arcmin, 8.6 arcmin, 13 arcmin or 17.2 arcmin). The dots within each square move with equal speed.

The task was to determine whether the dots in the two squares moved with the same speed. The viewing time was 4 s for each trial. There were 30 trials: in 15 trials the speed was the same in both squares, and in the other 15, the speed was different. In all cases the direction remained random. The speeds values were: 1.5°/s, 2°/s, 4.5°/s, and 6°/s. The ratio of the difference in speed between the two squares was the following: 1 when the speeds were equal; 1.33, 2.2 and 3 when they differed. The reference speed was 2°/s.

4.2.2 Results and Discussion. For each subject group the mean percentage scores of correct responses is portrayed in Fig. 2b. The Kruskal-Wallis test on the overall mean correct responses was used to compare the three groups and the results showed that they were significantly different ($\chi^2 = 12.08$, DF $= 3$, $p < 0.0071$). The Wilcoxon test was further applied to compare the performance of the ROP and the ROT groups. The ROP's were significantly worse than the ROT's ($Z = -2.21$, $p < 0.0119$).

I suggest that the marked deficit of the right occipito-parietal patient group on this task may be explained as a failure to obtain the global speed field or to compare their magnitudes. Inspection of the raw data indicated that every subject in the ROP subject group failed to discriminate reliably speed differences for ratios less than 3.

4.3.1 3D-Structure-from-Motion. This experiment, adapted from Ullman (1979) addressed the subject's ability to recover three-dimensional structure from motion cues alone. The motion was presented as a sequence of discrete frames, each frame depicting a collection of 32 unconnected elements. The 3-D coordinates of all the elements are stored in the computer memory, and their projection on the frontal plane was computed and displayed on the monitor. Figure 3 a shows an example of the display. The elements are lying on the surface of an invisible cylinder with radius of 4.4° and height of 5.7°. When the changing projection is viewed in a movie-like fashion, the elements in motion across the screen are easily perceived as a rotating cylinder. Each single static view of the cylinder (each frame) appears as a collection of random dots.

The imaginary cylinder is rotated by 5° degrees at a time, and its new projection is computed and displayed on the computer monitor. The cylinder revolves at a fixed angular velocity of 40°/s. The horizontal velocity of the projected points varies with their horizontal location on the screen. Points at the center move fastest, whereas points at the edges move slowest. The ratio between the maximum and minimum speed of the dots is 6.

The subject is asked to press a specially designated key on the computer key board when he can perceive a structure and to name or describe verbally the perceived structure. The maximum display time is 90 s.

4.3.2 Results and Discussion. There was only a single trial and the answers were scored as correct or incorrect assuming that the subject either identified the cylinder-like structure or did not. The results are

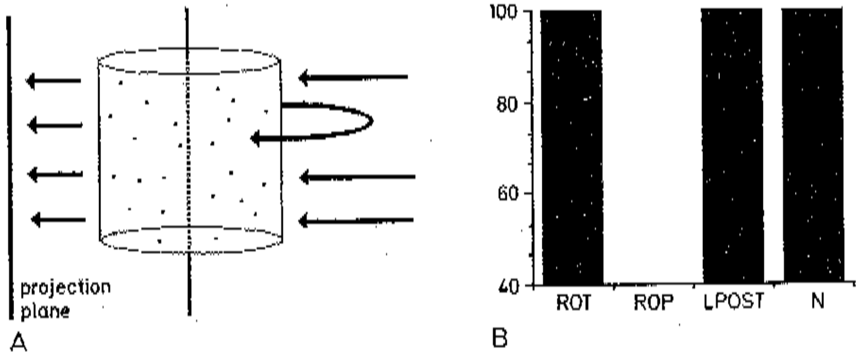

Fig. 3A and B. Structure-from-motion task. **A** The display consisted of the orthographic projection of a rotating cylinder defined by dots lying at random locations on its transparent surface. The outline of the cylinder was not presented in the actual task. There was one trial. The subject was asked to report verbally: (*1*) whether the display could be interpreted as a three-dimensional object in motion; (*2*) the direction of motion; (*3*) describe (or name) the object perceived. **B** Correct responses (there was only one trial) for the structure-from-motion task. The responses of the four subject groups are the following: (*a*) normal controls: 6/6; (*b*) left posteriors: 8/8; (*c*) right occipital-parietal: 0/5; (*d*) right occipital-temporal: 5/5

presented in Fig. 3b. None of the ROP subjects were able to carry out this task, while all but one of the subjects in the other lesion groups could do the task.

Experimental and theoretical studies have demonstrated that a three-dimensional structure can be established from displays consisting of unconnected elements in motion, and this interpretation requires neither familiarity with the object nor a priori recognition of the moving object (Wallach and O'Connell 1953; Johansson 1973). The question addressed here was whether focal brain damage to the posterior brain may disrupt the ability to recover structure from motion cues alone.

The experimental task was restricted to the perception of rigid objects. Subjects were asked to respond whether the set of moving dots evoked a simple three-dimensional object (a cylinder). The control group, the Left Hemisphere and the Right Occipito-Temporal patients groups had no difficulty perceiving the rotating cylinder, and all the subjects described seeing in the display either a "rotating cylinder" or a concrete familiar (cylindrical) object such as a "rotating lamp shade", "garbage can", or "revolving door". In contrast, the right occipito-parietal group typically responded that all that they saw on the display was "a bunch of dots moving", "ants crawling around on the ground", "mosquitos or flies", or "birds high in the sky" (Vaina 1988b). In no case did verbal cueing from the examiner help them to perceive a three-dimensional structure.

Looking more closely at the subjects' verbal responses it is apparent that the group with right occipito-parietal lesions failed to achieve a perceptual grouping of elements moving together as a rigid three-dimensional object. They instead reported having the impression of an incoherent collection of elements moving independently in the display.

It is possible that the occipito-parietal group may have failed either on the task of *computing motion* or failed in the subsequent task of using the motion measurements for recovering *structure from motion*. The results of several theoretical and experimental studies suggest that 3-D structure from motion can be computed from image motions derived from more complex (non-intensity based), visual elements and it is possible that the depth effect may be based on the preservation of these entities in successive frames.

5 General Discussion

5.1 Main Results

This investigation reports the segregation of deficits on stereopsis and on aspects of motion analysis in patients with unilateral lesions in the posterior right hemisphere. The patients, selected on the basis of the anatomical locus of the lesion, normal acuity and the ability to discriminate motion were assessed on three tasks of motion perception: *2D-Form-from-Motion, Speed Discrimination, and Structure-from-motion.* The first motion task is a task of *segregation* while the others are tasks of *integration*. The subjects were also assessed on Julesz' random dot stereograms for evaluating binocular stereopsis.

The right occipito-parietal (ROP) group was dramatically impaired on the Speed Comparison task and they completely failed on the Structure from Motion and the Stereopsis tasks. I have suggested that their deficit may be explained as a failure at the level of *integration* either in space (the total failure on the stereopsis task) and in time (motion frames). They had no difficulty, however, on the *2D-Form-from-Motion* task. The right occipito-temporal (ROT) patients group presented exactly the opposite pattern of deficits. They showed no significant deficit on the two

Table 2. Summary of the results on the stereopsis and visual motion tasks for two subject groups: patients with right occipital-temporal and patients with right occipital-parietal lesions. The first coloumn lists the psychophysical tasks. The second coloumn lists the suggested subtasks involved in carrying out the psychophysical tasks. The third and fourth coloumns indicate, for each of the two patients groups, whether they achieved (+) or whether they failed (–) the subtasks

Task	Subtasks	ROP	ROT
Stereo	Correspondence	–	+
	Coarse form	–	+
	Form	–	–
2D-form from motion	Twinkling motion (LR)	+	+
	Transl. motion patch	+	+
	Coarse form	+	+
	Form	+	–
Speed comparison	Local motion	+	+
	Global speed field	–	+
	Comparison speed fields	–	+
3D Structure from motion	Local motion	+	+
	Correspondence	–	+
	3D structure	–	+

tasks of *motion integration* (*Speed Discrimination* and *Structure-from-motion*). They were severely impaired on the tasks of identification of the form of two dimensional patterns from stereopsis and motion although in both cases they were able to achieve coarse figure-ground segregation.

Each of the experimental tasks presented here consists of several specific subtasks which may be resolved at different stages during visual processing. The pattern of deficits of the ROP and the ROT subject groups on the subtasks that may be involved in the motion and random-dot stereopsis experiments are summarized in Table 2.

We see that both groups were able to obtain local motion measurements. The ROT group was able to carry out the motion correspondence tasks, the computation of the global speed field, and, finally, to derive structure from motion and to compare global speeds. They were also able to obtain coarse form both from stereopsis and motion, but failed to integrate the information for extracting the exact, detailed contours of the forms. The ROP group failed on the speed discrimination and structure-from-motion tasks and on the stereopsis task. It is plausible that their deficits on these two motion tasks might have resulted from an inability to measure speed, or to use explicitly the speed measurements for obtaining speed gradient (in the Speed Discrimination task) and for the recovery of 3D-structure from motion.

The subsets of the Performance IQ test battery were not significantly correlated with the *Speed comparison* and the 2D-*Form-from-motion* tests (by the Pearson statistical correlation), or with the Stereopsis and the Structure-from-Motion tests (by the Spearman statistical correlation). Thus, among the neuropsychological assessments of perceptual abilities, the subtests of the WAIS-R, and perceptual tasks discussed in this study, should be considered as complementary.

5.2 *Two Systems for Interpreting Visual Information in the Human Brain*

Clinical neurological reports indicate that the early stages of visual processing are carried out bilaterally. The specialization of the posterior right hemisphere for visual-spatial tasks whose goal is to achieve a perceptual categorization of the visual information occurs in later stages (Warrington 1988; Vaina 1989). I propose that motion tasks of *separation*, which the detection and the local measurement of visual motion are part of the early, bilaterally supported processes. The patients studied in this investigation showed no evidence of primary sensory impairment on the tasks of detection of motion and the processes involved in the coarse separation of a figure from the static background by stereopsis or motion.

A double dissociation of deficits was obtained in the subjects with posterior right hemisphere lesions leading to two anatomically (subjects with occipito-parietal lesions and subjects with occipito-temporal lesions) and functionally defined subgroups. The subjects with right occipital-parietal lesions failed on tasks of stereopsis, speed discrimination and the recovery of structure from motion, but they showed no deficits on tasks of extracting form from motion. The subjects with right occipital-temporal lesions, on the other hand, showed no deficits on the speed discrimination and the recovery of structure-from-motion tasks, but they were severely impaired in extracting form from motion. I suggest that this double dissociation is routed in the following processes: (*1*) the measurement of depth and speed of motion, and the use of speed for further integration tasks; and (*2*) integration of local information into coherent boundaries. The right occipital-parietal patients were impaired on the first, while the right occipital-temporal patients were impaired on the second.

These results may be interpreted in the framework of the two cortical visual systems proposed in studies by Ungerleider and Mishkin (1982) and refined by Ungerlider and Desimone (1986). These two studies have demonstrated that the processing of an object's qualities and its spatial location depend on processing of different kinds of information in the posterior temporal and the posterior parietal cortex, respectively. The functional and anatomical dichotomy of the

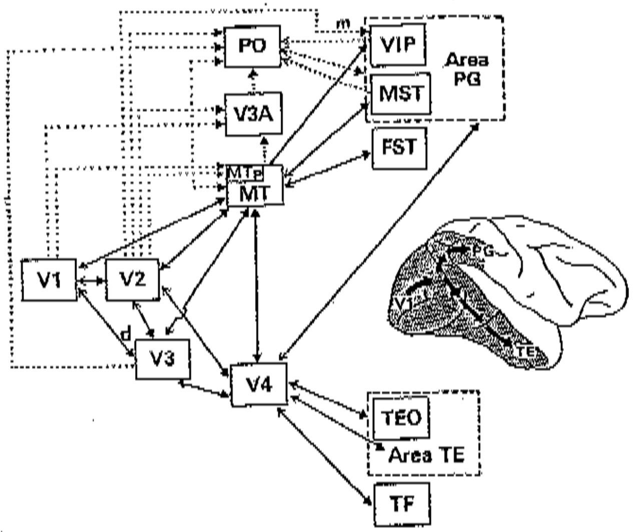

Fig. 4. Summary of visual cortical areas and their connections (adapted from Ungerleider and Desimone 1986). The heavy arrowheads indicate known *forward* projections and the light arrowheads indicate known *backward* projections. Dotted lines indicate projections that arise from the peripheral field representations. The figure shows that area MT provides a major route from the striate cortex into the parietal lobe and that it has heavy reciprocal connections with several other visual areas

interpretative visual processes, suggestively called the "*What*" and the "*Where*" pathways, is robust and it has been extensively documented in both humans and subhuman primates (for a review see Vaina 1989). The picture emerging is that of two main visual pathways, both originating in the primary visual cortex and following distinct routes into the temporal and parietal lobes (Fig. 4).

The several visual areas which are organized along these two pathways seem to be selectively specialized for processing information about the *form* or the *spatial* aspects of the visual input. A finer grained map of the visually responsive cortex distinguished several streams of processing, one involved in visual motion analysis, and another in the analysis of form (for a review see Maunsell and Newsome 1987; Maunsell 1987). Both the coarse and the fine grained views of cortical visual information processing converge to suggest that the processing of depth and of different aspects of visual motion are associated with visual areas situated along a dorsal path from the primary visual cortex into the posterior parietal lobe, the *Where* system. Information about form on the other hand is processed along a ventral route into the posterior temporal lobe, the *What* system.

Interpreted in this context, the results presented here suggest that the tasks of motion *integration* (tasks of grouping) such as the tasks involved in the structure-from motion and the computation of speed gradients, would be preferentially solved by the posterior right hemisphere along the occipito-parietal pathway, the *Where* system. Tasks which involve the integration of the local measurements of instantaneous motion or stereopsis into the *specific* form of the stimulus are part of the *What* system primarily involving the posterior temporal areas.

5.3 Computational Psychophysics

It is plausible that different motion systems may be involved in solving the tasks discussed in this investigation, and they may be mediated by different visual structures. There is evidence (Braddick 1974, 1980) that at least two systems may be involved in the measurement of visual motion in the human visual system. One system, termed *short-range process*, may be involved in computing the instantaneous local motions (displacement < 15 min arc). The second type of motion process, termed by Braddick *long-range*, analyses motion over larger temporal and spatial intervals in which there is no continuous motion of elements across the image to be measured directly.

In all the patient groups involved in this study, the lesion spared the primary visual cortex, and none of them had subsequent deficits on the tasks of local motion measurements *(short-range process)*. All the subjects were able to detect motion, and to achieve coarse figure/ground segregation of moving patterns in a static random dot background. However, the right-occipito-temporal group was unable to integrate this local information about boundaries into the exact shape. The computation of precise form must rely on using specific *form processes* which presumably were impaired with right occipito-temporal lesions.

A higher level motion system is involved in the recovery of three-dimensional structure and the computation of the global speed fields, which both require the *integration* of several measurements. The data reported here indicates that performance on such tasks is affected selectively by right occipito-parietal lesions. Common to these integration tasks is a general *process of grouping* defined by image features of different complexity depending on the task at hand. Examples of underlying mechanisms that have been proposed are processes of correspondence and of the recovery of three-dimensional structure which use computational schemes that are not local and instantaneous (Braddick 1974; Marr 1982; Ullman 1979, 1983), but use information that is extended in space and time. Another possibility is that the processes of integration take simpler measurements as an input and compute the global motion of the combination.

5.4 *Physiological Considerations*

Anatomical and physiological studies have demonstrated the existence of a multistage motion analysis system in the primate visual cortex. The first stage is the striate cortex (layer 4B) and specific anatomic subdivisions of V_2 (the thick cytochrome oxidase stripes). These regions project further to the middle temporal area of the extrastriate cortex (MT), located in the posterior bank of the superior temporal sulcus (Zeki 1978; van Essen 1985), which, in turn, transmits motion information to visual areas in the posterior parietal lobe such as MST and VIP. The striate (area V_1 or 17) neurones are optimally sensitive to lower speeds (to about 32°/s), whereas the MT neurones respond optimally to higher speeds. MT neurones are also highly selective for the direction of stimulus motion, binocular disparity and orientation among other properties (Dubner and Zeki 1971; Maunsell and van Essen 1983; Albright 1984, Rodman and Albright 1987). The role of these latter areas in motion processing it is less well understood. It is known, however, that neurones in these areas respond to even more complex motion patterns, such as to flow patterns generated by an observer moving through the environment, for example.

The subjects included in this investigation had lesions in the posterior right or left hemisphere, in all cases sparing the primary visual cortex. As expected, they were able to carry out measurements of the local velocity field which constitute the first step of computation in all the motion experimental tasks addressed in this study. I suggested that the deficit of the occipito-parietal group on the two motion tasks might be a failure at the level of motion *integration*. That is, the *speed comparison* task and the *structure-from-motion* may involve the integration of the output from several simple and local computations.

Studies of stereoscopic vision in alert monkeys unequivocally demonstrated that a large number of cells in $V1$ and $V2$ are sensitive to horizontal disparities of the type addressed in this study (Poggio and Fischer 1977). This makes our results on the random dot stereograms test intriguing for neither group of right posterior subjects performs well on this task although their lesion areas did not involve the most posterior areas of the visual cortex. It is possible that stereo correspondence occurs later on (e.g. in MT), and that there might be a back projection to the primary visual cortex which by and large resolves the coarse stereopsis task. This hypothesis is supported by the experimental results reported here which revealed the inability of the right occipito-parietal group to do the stereopsis task and the partial deficit of the right occipito-temporal group who only obtained a "coarse" stereopsis.

Recent PET scan studies in humans (Miezin et al. 1987; Allman 1988) suggested that the human homolog of MT may be located in the fundus of the temporal occipital-parietal pit (TOPF) (see Fig. 271 in Polyak 1957). The neural circuitry subserving this region appears to be included in the bilateral lesion found in Zihl's patient and in the subjects with right occipito-parietal lesions reported here. However, some of the lesions in our patients (in Zihl's patient as well) were moderately large and involved much of the white matter, thus it is appropriately cautious to stress that the lesions extended along the motion pathway, thus involving among several other areas, including the homologue to MT.

5.5 *Comment on the Possible Role of MT*

Considered as computational problems (Marr and Poggio 1979; Ullman 1979; Marr 1982) *stereopsis* and *structure-from-motion* have characteristically been regarded as containing a common subproblem, the computation of *correspondence* between elements in different frames. It is thus possible to conjecture that one of the roles of MT might be to host some kinds of correlation processes (e.g. "the correspondence process") between elements or groups of elements over time or space. The nature of the *correspondence process* remains a mystery although many have considered the problem from a variety of perspectives. These include contributions by Ullman (1979, 1983), Todd (1984), Braunstein and Andersen (1984), and Prazdny (1986) to name only a few. Of particular interest is Prazdny's experimental work which suggests that stereopsis and the structure-from-motion problems are solved by mechanisms which are qualitatively different from each other. Binocular stereopsis is a depth measurement device and thus its role is to inform the visual system about "absolute" and "relative" depth relationships. Stereopsis is effective in the "reach-space" (Vaina 1989), that is, for assessing distances reachable by hand. Structure-from-motion, on the other hand, provides only relative depth information on elements of the same 3D object, and hence it is a "spatial layout mechanism" (Prazdny 1986) and it is not related to the computation of distance. If these assumptions were correct, and as there is some evidence that MT area might be involved in computing both structure-from-motion and stereopsis, it is possible that it actually may compute the relative depth of elements. Whether these elements are local features, clusters of features or perhaps global regions is not yet clear and calls for further investigation.

Consider either Marr's (1982) and Ullman's (1979) correspondence hypothesis, or Prazdny's relative depth relationship hypothesis, together with Adelson and Movshon's "plaid" motion pattern result. A possible role of MT which emerges from these hypotheses, is to achieve some type of *perceptual grouping* based on the *integration* of elementary and local measurements. Siegel and Andersen (1986) reported that, in behaving rhesus monkeys, lesions to MT impair the perception of rigid structure from motion[4]. Thus MT may be involved in computing a qualitatively different information, a *composite measurement*, which characterizes more complex aspects of motion. This view is consistent with the network of anatomical connections of MT. Thus Fig. 4 above shows that MT is reciprocally connected with many visual areas, which would be appropriate for establishing correlations between elements of different nature and complexity. Specifically relevant for this discussion are the reciprocal connections between MT and V_4 and between MT and V_2 and V_1 suggesting that many of these computations would involve feedback projections from MT or V_4 to V_1 or V_2. Thus V_4 and MT may interchange more complex information about coarse borders, whereas V_1, for example, would convey more primitive and rough information.

The anatomical data on the subject population involved in this study is consistent with an involvement of the human equivalent of area MT in the lesions to the occipito-parietal area and this may account[5] for their failure on the correspondence and motion integration tasks involved in stereopsis, recovery of rigid structure from motion, and perhaps in the comparison of the global "speed fields".

6 Concluding Remarks

The main finding of this study is that damage to the right occipito-parietal area tends to selectively disrupt several aspects of motion analysis and stereoscopic vision, while lesions to the right occipito-temporal area do not. Lesions to the right occipito-temporal area, but not lesions to the right occipital-parietal area, interfere with the ability to extract the exact form from both motion or stereopsis.

These findings are consistent with the functional specialization demonstrated in the visual cortex of subhuman primates, which have revealed specialized streams of processing devoted to specific aspects of motion or form.

The results on the motion and stereopsis tasks presented in this study suggested that the solution to the problems of stereopsis and aspects of motion integration involves correlation processes which operate in extended space or time.

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[4] The results of this study must be taken with caution, however. It is not clear whether the monkeys perceived structure-from-motion or a global speed field

[5] One must be cautious, however, speculating on the basis of the primate brain and generalizing to humans only on the basis of a small number of cases. Moreover one must be guarded in advancing the hypothesis that motion deficits, such as those discussed in this study, are uniquely lateralized to the posterior right hemisphere. The lesions included in the left hemisphere group were less well delineated than the right hemisphere lesions. The dissociation obtained in the right hemisphere group is, however, robust and strongly suggests that these questions should be further pursued and the results replicated in a larger patient group. One of the issues that should be carefully explored is that of "covert" bilateral lesions, which are not uncommon after basilary artery events, for example. This issue is currently being pursued in my laboratory in a patient population characterized radiologically by high resolution MRI studies

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