

Complex motion perception and its deficits

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Within the hierarchy of motion perception, the dorsolateral middle superior temporal area (MSTd) is optimally suited for the analysis of the complex motion patterns that are directly useful for visually guided behaviour (e.g. computation of heading). Recent electrophysiological and psychophysical evidence suggests the existence of 'detectors' in MSTd that are specialised for complex motion patterns and advocates the necessity of combining retinal and extraretinal signals received by MSTd neurones for the accurate perception of heading. In some neurological patients, of which only a small number have been reported to date, lesions involving the human homologue of MST have devastating effects on their ability to navigate in their surroundings. It has been reported that these patients have impaired performance of psychophysical tasks of complex motion discrimination.

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Abbreviations

COM	center of motion
MST	middle superior temporal area
MSTd	dorsolateral MST
MT	middle temporal area
V1	primary visual cortex
VIP	ventral intraparietal cortex

Introduction

Among the areas of the extrastriate visual cortex that are particularly well suited to the analysis of visual motion are the middle temporal area (MT) and the middle superior temporal area (MST), as has been shown by single-cell recordings in monkeys. Hierarchical processing takes place in areas MT and MST, such that MT neurones are selective to direction of translation while MST neurones are selective to more complex motion patterns, such as radial, circular and spiral motions [1–6]. In macaque monkeys, the functional architecture and anatomical connections of area MT, its contributions to visual motion perception, and the specific motion deficits resulting from partial or total ablation are reasonably well understood and have been reviewed abundantly. More recently, research has focused on the properties of MST and its role in perception, as it is the next area in the visual motion hierarchy.

In this review, which is directed at the neural and psychophysical correlates of visually guided behaviours, I will concentrate on the behaviourally relevant properties of this later stage in the motion processing hierarchy, particularly the dorsolateral region of MST (MSTd). Its neurones preferentially respond to patterns of motion within the receptive field, and because these patterns are often generated by self motion, they are useful for navigation and can indicate unambiguously the movement of objects relative to the viewer, something that neurones in earlier stages of the visual pathway cannot do.

Perception of motion for visually guided behaviour

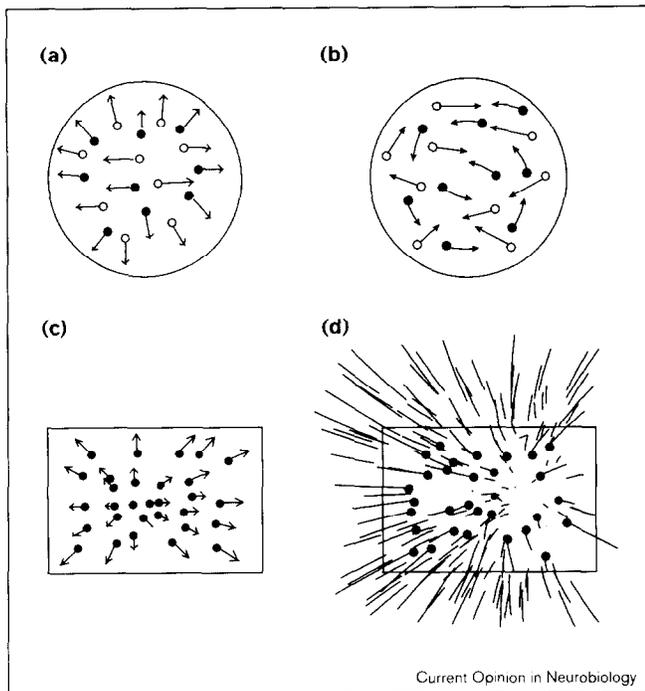
As we move through the environment, the pattern of visual motion on the retina provides rich information about our passage through the scene. This information, termed 'optic flow' [7], is indispensable for encoding self-motion, orientation and visual navigation in three-dimensional space, for the perception of object movement, for stabilising the visual world, and for controlling posture and locomotion. Gibson [7] proposes that the computation of optic flow must be mediated by high-order mechanisms that detect "perceptual contact with the surrounding world". The nature and properties of the mechanisms involved in the perception of optic flow have been studied using both physiological and psychophysical techniques.

Physiology of optic flow

Cells in MSTd have been found to respond selectively to expansions, contractions, rotations [1,2,5,8,9], spirals [6], and to multi-component (i.e. plano-radial, plano-radial-circular, etc.) [3,4,10] motions. This makes them better candidates for the computation of optic flow than the directionally tuned neurones earlier in the motion hierarchy, such as the neurones in primary visual cortex (V1) or MT, whose much smaller receptive fields 'see' only a limited fraction of the visual scene and respond to relatively simple motions in a single direction. Neurones in MSTd are well suited for the analysis of complex optical flow patterns (examples are shown in Figure 1), as they respond best to large stimuli, indicating extensive spatial summation [2–5,11]. They have large receptive fields (with a mean diameter of 60°), many of which extend over both contralateral and ipsilateral visual hemifields. In these neurones, there is no strong correlation between receptive field size and the retinal eccentricity of the center of the receptive field.

The response of MSTd neurones is insensitive to stimulus position and image-element density over a broad range, and nearly 90% of the MSTd neurones studied prefer stimuli containing a speed gradient to those in which all

Figure 1



Schematic views of typical complex motion stimuli. **(a)** Radial motion (portraying expansion). **(b)** Circular motion (portraying counterclockwise rotation). **(c)** Heading (translation). **(d)** Heading (curved path).

image-elements move at the same speed [12^{••}]. This combination of sensitivity to patterns of speed and patterns of directions, absent in earlier visual areas, strengthens the view that MSTd is involved in analysing optical flow and representing the structure of the three-dimensional visual environment.

MSTd cells have a particularly strong bias for expanding motion, suggesting that this area plays an important role in visually guided navigation, as forward motion through the world produces a significantly higher proportion of expanding than contracting patterns of optical flow on the retina.

MSTd neurones have the necessary characteristics to compute the direction of self-movement (heading) [13^{••},14], and signals representing heading directions are anatomically clustered [15]. When the observer translates and the eyes are still, the recovery of heading direction from visual motion results from locating the focus of expansion in the optical flow field. To achieve this computation, neuronal responses must vary with the position of the motion stimulus within the receptive field. Graziano *et al.* [6] have reported that for preferred stimuli, the responses of MSTd neurones exhibit position invariance to small shifts in the center of motion (COM). Using larger shifts and larger stimuli [14,16], position invariance appears to be limited to a small region, beyond which the response

decreases with distance. MSTd is the first area in the visual motion pathway whose neurones have a direct role in perceiving heading [14,17].

Appropriately, MSTd neurones are also highly sensitive to extraretinal information about eye movements. When eyes move, their retinal COM shifts away from the direction of heading. It has been demonstrated that many MSTd cells are tuned for heading stimuli and that their tuning interacts with pursuit eye movements [18^{••},19]. Lappe *et al.* [18^{••}] demonstrated that radial optic flow fields simulating self-motion (i.e. heading) elicit optokinetic eye movements linked to the direction of gaze.

Several neuronal strategies have been proposed to explain how MSTd neurones analyse optic flow. A common denominator in all explanations is the provision of velocity selectivity from MT cells to MSTd [20,21]. One mechanism [9] assumes that each MSTd cell—each of which is responsive to a particular complex motion trajectory—integrates inputs from an array of MT cells with the appropriate distribution of receptive fields (e.g. MSTd cells tuned to radial motion integrate inputs from MT cells whose receptive field positions and preferred directions are arranged radially). Positional invariance of directional selectivity within the large receptive field of an MSTd cell is obtained by postulating that its receptive field consists of several compartments, each performing integration within its own small territory, independently of the other compartments [1]. This mechanism, however, cannot account for the finding that the responses of many MSTd neurones are not limited to pure radial motion, as they often respond to two or three components of motion (e.g. planar and circular, or spiral, which results from the combination of radial and circular motion). An alternative possibility is that MSTd neurones use a feature-matching strategy, whereby individual neurones represent particular optic flow fields. For example, a flow field combining planar, circular and radial motion could be represented by a specific set of triple-component neurones. Another plausible strategy involves population coding, whereby optic flow is computed by a large number of MSTd neurones acting in concert. The frequently noted redundancy in cortical information processing makes it conceivable that these latter two strategies coexist.

It should be noted that area MSTd is not the only cortical region responding to aspects of optic flow. Recent studies have demonstrated that other areas in the parietal lobe, such as the ventral intraparietal cortex (VIP) and area 7a, are highly sensitive to optic flow stimuli [22[•],23[•]]. It is likely that higher-level motion, similar to the translational global motion (motion coherence) primarily studied in area MT, is mediated by several higher-level motion-responsive cortical areas. It is possible that the particular way in which optic flow is defined may activate neurones in different areas. For example, stimuli simulating rotation of a plane in three dimensions (e.g. fanning displays) activate

neurones in VIP [22•,23•]. In the lateral intraparietal cortex (LIP), optic flow selectivity is modulated by the locus of the optic flow and eye position. One should bear in mind that the areas exhibiting optic flow selectivities are anatomically connected to MST, which suggests that this selectivity may be transferred from MST, and that the higher areas in the motion system may both elaborate on the properties of optic flow represented and concentrate more on the integration of the optic flow signal with motor and spatial signals. To create an abstract representation of space, the posterior parietal cortex combines signals from many different modalities, such as visual, auditory, somatosensory and vestibular signals. It is possible that our unitary perception of the space around us, independent of the sensory modality, is embodied in this abstract representation of space in the posterior parietal cortex [24••].

Psychophysics of optic flow

Recent psychophysical studies have demonstrated the existence and characteristics of complex motion detectors. In these studies, optic flow information is used for perceptual tasks underlying visually guided behaviours.

The sensitivity of the human visual system to optic flow stimuli has been studied by psychophysical means. To investigate whether higher cortical areas might be involved in the processing of complex motion patterns, Steiner *et al.* [25] studied the degree of interocular transfer of expansion, rotation and translation motion aftereffects. They found that in visual cortical areas beyond V1, almost all cells are binocular, whereas in V1, many are monocular. They also found that the degree of interocular transfer was greater for aftereffects of expansion and rotation than for translation, suggesting that higher visual areas are involved in motion aftereffects to complex motion sequences. A recent study by Takeuchi [26•] suggests an asymmetry between the processing of expansion and contraction during a visual search task. In human subjects taught to search for an expanding target among contracting distractors, the time needed to find the target does not vary with the number of distractors. However, the search time for a contracting target among expanding distractors does increase as a function of the number of distractors. The author concludes that expansion and contraction are processed by higher-order units in the visual system that respond asymmetrically to expansion and contraction [26•].

Several recent studies have provided evidence for the existence of detectors specialised for radial motion, also known as looming detectors. Specialised mechanisms for complex motion have been suggested by a series of masking studies and adaptation studies that propose the existence of mechanisms selectively sensitive to expansion or rotation distinct from the basic motion mechanisms that signal change in speed or linear direction [27–31,32•,33]. However, as the physiology suggests, the mechanisms that respond specifically to complex motion occur at a relatively

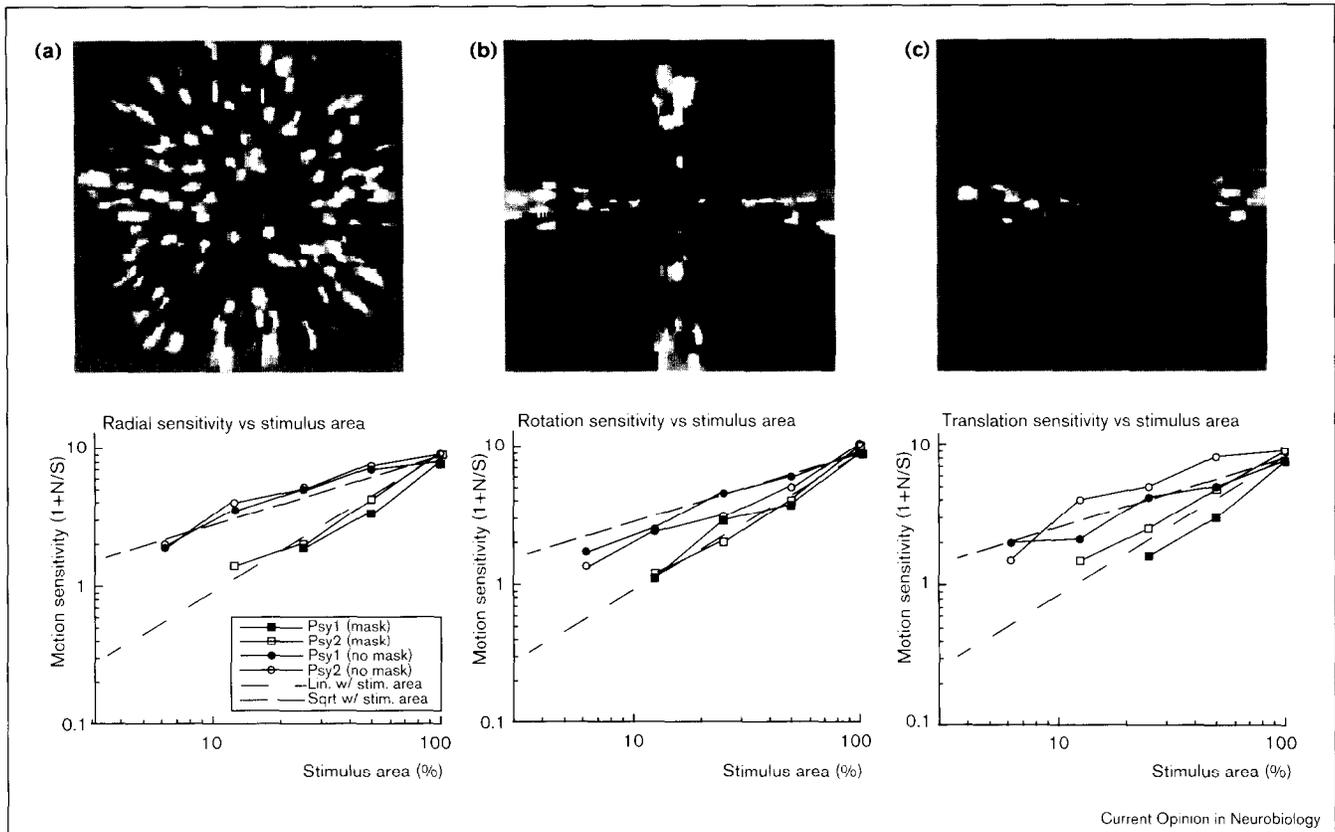
high level of analysis in the brain (i.e. MST); it is not clear that the techniques described above will necessarily probe this site. Adaptation and masking may influence the response of MST neurones, but they may also influence the response of neurones at earlier sites (such as V1 or MT), and this may complicate the interpretation of the results [34,35••].

To investigate the putative perceptual attributes of area MSTd, my colleagues and I [34] have applied a summation technique to study mechanisms tuned to optic flow fields presented as random-dot cinematograms producing radial, circular or translational motion within a circular aperture spatially curtailed into symmetrically opposed sectors (Figure 2, top row). Because the signal-to-noise sensitivity (i.e. the inverse of the minimal proportion of coherently moving dots at which direction of motion is discriminated reliably) increased with the stimulus area for all three types of motion (which is consistent with an ideal integrator model of motion sensitivity), we reasoned that motion of opposing directions must be integrated by specialised neural mechanisms (Figure 2, bottom row).

By contrast, sensitivity did not increase with stimulus area, which is consistent with the limiting of contrast sensitivity by an early level of processing, possibly V1 (Figure 2, bottom row). However, summation for contrast sensitivity did take place when the stimuli were very noisy, forcing the limit of sensitivity to be set by a later stage. The results fit well with the electrophysiological evidence for detectors of complex motion in MSTd, after contrast thresholding in V1. Using the same technique, we [35••] subsequently demonstrated that summation can take place over very large areas, consistent with the existence of optic-flow detectors with very large receptive fields, as suggested by physiological studies. Recent results from a psychophysical study of complex motion discrimination [36] suggest that the human visual system prefers radial motion (both expansion and contraction) compared to circular motion; this preference is maintained for the perception of the COM. The results of these and other psychophysical studies suggest that there are specialised cortical detectors that integrate local motions to obtain a global motion percept [35••,36–38]. An alternative view [39•] is that these computations are mediated by the interaction of local and global motion detectors.

Following recent physiological findings, several psychophysical studies, while assuming the existence of specialised detectors for complex motion, have attempted to characterise their sensitivity to speed. It has been reported that expanding dot patterns appear to move faster than rotating patterns, and that the magnitude of the illusion decreases when the number of directions defining the motion and the dot density are reduced [40,41]. In patterns in which only wedge-shaped sectors of the stimuli are presented, the difference in perceived speed increases with angular sector size [12••]. This finding suggests that

Figure 2



Motion sensitivity for direction of complex motion. The data (adapted from [34]) illustrate that motion sensitivity increases with stimulus area for all three types of motion tested: (a) radial; (b) rotation; and (c) translation. The squares in the graphs refer to the condition when the nonsignal sectors were set to average mean luminance (portrayed above) and the circles refer to the condition when the nonsignal sectors were filled with motion noise of the same statistics. The dashed lines represent the signal-to-noise ratios of an ideal integrator that sums the motion signals over the whole display.

the perceived speed depends upon the global pattern of motion of the stimulus. However, other experiments assessing speed discrimination thresholds for complex motion indicate that thresholds for expanding, rotational and linear motion are similar [42]. Furthermore, Sekuler [42] argues that the speed discrimination thresholds can be predicted on the basis of the pooling of unidirectional local motion signals. An intriguing view is that of Verghese and Stone [43–45], who suggest that speed discrimination depends on the parsing of the stimulus in terms of objects. In this framework, Sekuler's [42] data could be interpreted as the motion of single expanding and rotating objects. A different approach to the perception of speed in complex motion patterns has been taken by Bex and Makous [46••], who compared perceived speed of radial and vertical gratings. They found that the speed of radial gratings is consistently overestimated by 20–60% relative to translational gratings. They speculate that the greater apparent speed of radial motion is related to the apparent motion-in-depth of expanding and contracting patterns. This suggestion is consistent with our recent study

(CWG Clifford, SA Beardsley, LM Vaina, unpublished data) of perception and discrimination of speed of complex patterns.

Optical flow is a powerful cue for the perception of the direction of self-motion during navigation and locomotion [47,48]. The flow field is relatively simple when the observer translates towards a stationary scene while holding the direction of gaze fixed: the direction of heading is specified by the focus of expansion. Using random-dot stimuli to simulate optical flow patterns, Crowell, Banks and colleagues [49,50] have found that heading accuracies are less than 1° when the heading is near the line of sight, but increase as it becomes more peripheral. The estimation of heading is very precise in the presence of a ground plane, wall surface, or three-dimensional cloud [51]. Heading judgements are robust to noise in the visual stimulus, as demonstrated by psychophysical performance when the stimulus contains a proportion of randomly moving dots or by limiting the lifetimes of the dots conveying the heading information [52].

The problem of estimating heading becomes more difficult when the observer's gaze of direction changes over time because the rotation of gaze adds a rotational flow field created by the observer's translation; therefore, there is no longer a focus of expansion corresponding to heading. Psychophysical studies have demonstrated that heading computations during eye movements with small rotation rates are still highly accurate [53–56], whereas at higher rotation rates, information about eye movements becomes important. At high rotation speeds, if observers hold their eyes still, they perceive movement as a curved path; yet, if the rotation results from eye movements, then translational motion is perceived accurately [55,56]. Royden *et al.* [55,56] commented that when observers move their gaze, perception of heading requires the use of extraretinal signals. Addition of depth cues can enhance the perception of heading in the presence of noise or observer's rotations [57].

Clearly, viewing distance changes during heading, which must cause changes to the vergence angle between the eyes so that the fovea remains aligned as much as possible with the object of interest. In the context of radial optic flow, centrifugal motion increases the vergence angle, whereas centripetal motion decreases it [58*]. From the characteristics of the vergence induced by optic flow, Busetini *et al.* [58*] conjecture that vergence is actually a rapid ocular reflex that compensates for the translational disturbance of the observer, and that it is mediated by MST. The real world environment is cluttered with moving objects. Ideally, our heading judgements must be robust and should not be affected by the presence of static or moving objects. Psychophysical studies have demonstrated that if an object does not cross the observer's path, it has no effect on the observer's heading judgements [59,60]; however, when it does cross the observer's path and obscures the focus of expansion, there is a consistent bias in the direction away from the object's focus of expansion. This suggests that the visual system relies on a visible focus of expansion to make accurate heading judgements [50,61]. Royden and Hildreth [59] have shown that the direction of the judgement bias depends on the particular motion of the object: for horizontally moving objects, the bias is consistent with the object's direction of motion, whereas for objects moving in depth, the direction of the bias depends on the starting position of the object.

Deficits of complex motion perception in patients with extrastriate lesions

Almost no studies have examined specifically the ability of patients with extrastriate lesions involving the dorsal visual processing pathway to use optic flow for navigation. However, we [62] have recently reported deficits in complex motion (including heading, radial and spiral motion) perception in two stroke patients (patients RR and CMK), who had bilateral occipital–parietal lesions and who were recovering from Balint–Holmes syndrome. Both patients performed well on tasks of low-level

motion, such as direction discrimination and perception of two-dimensional form from direction or speed differences. Patient RR [62] had difficulties navigating in his wheel chair (for reasons that could not be explained by any motor disorder), and frequently bumped into people, corners, and things in his way, particularly into moving targets (e.g. people walking). He was unable to catch a ball or any object thrown directly to him, whatever its speed; although he could see the object and that it was moving. In the laboratory, he was unable to perceive radial motion and was very impaired on even the simplest heading tasks. His performance on radial motion discrimination was similar to that of patient LM, who had previously been described as 'motion blind' [63]. Patient LM's failure to discriminate radial motion should have been expected, were it not that she demonstrated good perception of 'biological motion', which is an example of high-level motion. It appears that patient LM could extract structure from motion (similar to the partially akinetopsic patient AF [64,65]), but she completely failed to discriminate motion in depth [66] (which was not tested in patient AF).

We (LM Vaina, ME Goldberg, unpublished data) have recently studied a patient referred to as patient CMK, who reported that she felt "uncomfortable walking, because she could not feel a stable system of reference around", and that her "posture was not stable". She felt very uneasy even standing, especially on the street or in traffic. She was unable to cross the street alone, as she could not judge whether cars were coming towards her. She saw them moving, but "had no feeling of what they were doing". She could not catch a ball or any object thrown at her, and reported that she had only a "vague impression that it was approaching". Initially, after her stroke, she suffered mild right-side neglect and could not manipulate tools, silverware, and instruments with her hands, in spite of not having any motor weakness. She recovered within a few weeks, but retained a selective deficit on some complex motion perception. She was severely impaired on any three-dimensional motion task, but her two-dimensional motion perception was good, even when dynamic noise was added to basic high-level motion stimuli, such as rotation. However, she could not discriminate radial motion, perceive the COM, heading or three-dimensional structure from motion. Patient CMK is uniquely interesting because her good performance on most low-level motion tasks contrasts with a complete failure on three-dimensional motion tasks, directly supporting a hierarchical organisation of the visual motion system.

It is not yet clear, however, how strict this hierarchy is and whether deficits of low-level motion necessarily affect perception of complex motion. The few neurological cases reported so far suggest this is not the case. We have described a patient referred to as patient AMG, who had a unilateral lesion in the left posterior parietal cortex and associated white matter and who had severe

early motion deficits, but whose performance on complex motion tasks was normal [67,68]. She was so severely impaired on a broad spectrum of visual motion tasks for stimulus presented in the contralateral field of her lesion that she spontaneously reported “I almost don’t see how things are moving”. In the visual field contralateral to her lesion, she could not discriminate speed of motion, plaid patterns, or extract discontinuities from motion. However, her perception of heading, radial and rotational motions were normal, as was her ability to discriminate directions in global motion (the motion coherence task adapted from [69]). These data suggest that higher-level motion tasks do not require very precise low-level computations or that additional mechanisms may be used to compensate for these deficits [70], which is compatible with the normal performance of patients AF and LM on certain higher-level motion tasks [65,66].

We [71] have recently described a particularly intriguing dissociation of performance on heading tasks and three-dimensional structure-from-motion perception in a patient referred to as patient RA. This patient had a unilateral lesion in the medial right occipital lobe, had no marked visual field deficits by neurological examination, and was severely impaired on several tasks of low-level motion for stimuli presented in the visual field contralateral to his lesion (i.e. discrimination of direction, speed, and two-dimensional form from motion). Perception of radial and circular motion were normal in each hemifield. Eye movements measured quantitatively were normal. He made accurate judgements of heading for translational motion in a stationary scene, but was severely impaired (in both hemifields) on three-dimensional structure from motion. It would appear that this patient can perceive the COM (in translational heading), but fails to perceive heading on a curved path for stimuli presented in either visual field. This result suggests two things. First, because judgement of straight-line heading was normal but three-dimensional structure from motion was impaired, it suggests that scene reconstruction is probably not necessary for straight-line heading judgement. Second, similar to the motion-impaired patients discussed above, patient RA’s normal performance on complex motion tasks, in the presence of impaired low-level motion, suggests that these higher-level computations do not depend on highly accurate low-level motion measurements.

A recent study [72] has reported false perception of motion in a neurological patient (referred to as patient RW), who had a bilateral extrastriate cortex lesion involving the presumed human homologue of MST. Patient RW suffered from a false perception of motion as a result of an inability to take eye movements into consideration when presented with self-induced retinal image slip. Haarmeier *et al.* [72] suggest that the patient’s deficit may be explained by a “disentangled self-induced and externally induced visual motion by comparing retinal signals with

reference signal encoding eye movements and possibly ego-motion”.

Pursuing in depth the ability of neurological patients with focal lesions to carry out optic flow computations would be extremely valuable to our understanding of this important aspect of visual motion perception. The study of neurological patients with selective perceptual deficits caused by focal lesions that can be related to established cortical maps offers a special non-invasive opportunity to establish functional roles for different areas of the human extrastriate cortex.

Conclusions

Recent physiological and psychophysical experiments have demonstrated the existence of specialised detectors for complex motion and have thoroughly characterised their properties and involvement in visually guided behaviours. However, as we have already seen, the study of retinal signals is not sufficient to elucidate the role of area MST and of other motion-responsive areas of the posterior parietal cortex in visually guided behaviour. Results from physiological and psychophysical studies are in agreement that in response to an extraretinal eye-movement signal, motion-sensitive neurones in MSTd shift their tuning properties spatially to compensate for eye movements (see e.g. [18•,55]).

Relevant to the topic of this review is the specific link between oculomotor behaviour [18•,73] and the expectation of a stimulus at a specific location or the prediction of a target location and movement [74,75]. An understanding of the interaction between retinal and extraretinal signals is particularly important for elucidating the neural substrates of heading and object motion perception.

Although much progress has been made toward understanding the neural substrate of optic flow, there are still many questions that remain unanswered. What properties do neighbouring neurones have in common? What is the role of the MSTd neurones in encoding heading and the effects of eye movements on heading perception? How are motion perception and eye movement combined? How is the perception of optic flow affected by eye movement deficits or by impairments on visual motion tasks mediated by neural circuitry situated lower in the motion hierarchy? And finally, and perhaps most difficult to address, what is the link between the neural activity underlying optic flow and sensory decision?

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