

Analysis of Self-Motion by Parietal Neurons

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Most animals, including primates and man, spend much of their time moving around in their environment. Sensing and controlling self-motion is an important requirement for a normally functioning and behaving animal. The last few years have seen primate neurophysiology starting to investigate the cortical mechanisms of self-motion processing. This paper presents a current view on how the determination and representation of self-motion in primate cortex is organized. It focuses on the visual information, i.e., the optic flow field. The literature on the processing of optic flow in the primate visual system is reviewed, and neurophysiological results are discussed in relation to computational requirements. Later, the integration of visual with nonvisual information supporting self-motion analysis is considered.

Multiple Sensory Signals Are Available During Self-Motion

For a complete description of self-motion, a number of different motions have to be considered. While the body translates and rotates in space, the head can move on the body and the eyes can move in the head. The central nervous system has a multitude of signals available for the determination of self-motion. These signals operate in various frames of reference. Otolith and labyrinth organs signal translation and rotation of the head in space. Somatosensory proprioception and sensorimotor feedback from the legs, trunk, and neck might be used to signal the direction of body motion during walking and the position of the head on the body. Eye muscle proprioception and motor efference can be used to signal the occurrence and velocity of eye movements. Nevertheless, in primates vision probably provides the most important signal for self-motion determination. Visual input often dominates other sensory signals. It can elicit postural responses and induce the sensation of circular, linear, or curvilinear self-motion (Dichgans and Brandt 1978; Lee 1980; Lestienne et al. 1977; Sauvan and Bonnet 1993). Visual input can also be used for the accurate estimation of self-motion parameters such

as the time-to-contact with an obstacle (Regan and Hamstra 1993) or the direction of heading (Warren et al. 1991; Warren and Hannon 1990).

The importance of the visual input for the estimation of self-motion has first been pointed out by Gibson (1950). He introduced the term optic flow for the motion in the optic array surrounding a moving observer. This optic flow field in Gibson's sense thus describes the self-induced motion of the visual world in a body-centered reference frame. The optic flow carries information about self-motion parameters and also about the spatial relationship of objects in the three-dimensional world. The latter is conveyed by motion parallax. Motion parallax is the difference in the apparent motion of two objects positioned at different distances from the observer. Near objects appear to move faster than objects located further away. With respect to self-motion, Gibson noted that for a translating observer the motion in the optic array contains a singularity he termed the "focus of expansion" that lies in the direction of heading. The term "singularity", or "singular point", refers to an idealized point in the flow field at which visual motion is zero, i.e., a point that remains stationary in the optic array. For an observer moving on a straight line, the destination of travel is such a point, because all visual motion seems to expand radially from this point. Gibson's suggestion that the visual system might directly use this singularity to determine the direction of heading by analyzing the global optic flow structure has started a long line of research on optic flow perception that still continues to pose new questions to psychophysicists, computer scientists, and, as of recently, neurophysiologists.

Retinal Optic Flow Is a Complicated Self-Motion Signal

The analysis of motion in the optic array is complicated by the fact that the visual system senses movement in the optic array by virtue of the retinae, which are movable sensors themselves. Thus, movements of the retinae, i.e., eye movements, superimpose onto movements in the optic array. The result is a confounded flow field in which the focus of expansion is often obscured (Koenderink and van Doorn 1981; Nakayama and Loomis 1974; Regan and Beverly 1982). The visual system has to work with this retinal flow (Warren and Hannon 1990) as input and develop methods to deal with the influences of eye movements.

The potential complexity of the retinal flow field is illustrated in Figure 1. Several examples all describe essentially the same body motion. An imaginary observer moves on top of a ground plane covered with visible features schematized as black dots. Moving forward, he gazes at some point in space (Fig. 1a). The distinction between the direction of gaze and the direction of movement is very important. The direction of gaze defines the center of the retinal coordinate system in which the retinal flow is eventually represented, while the direction of

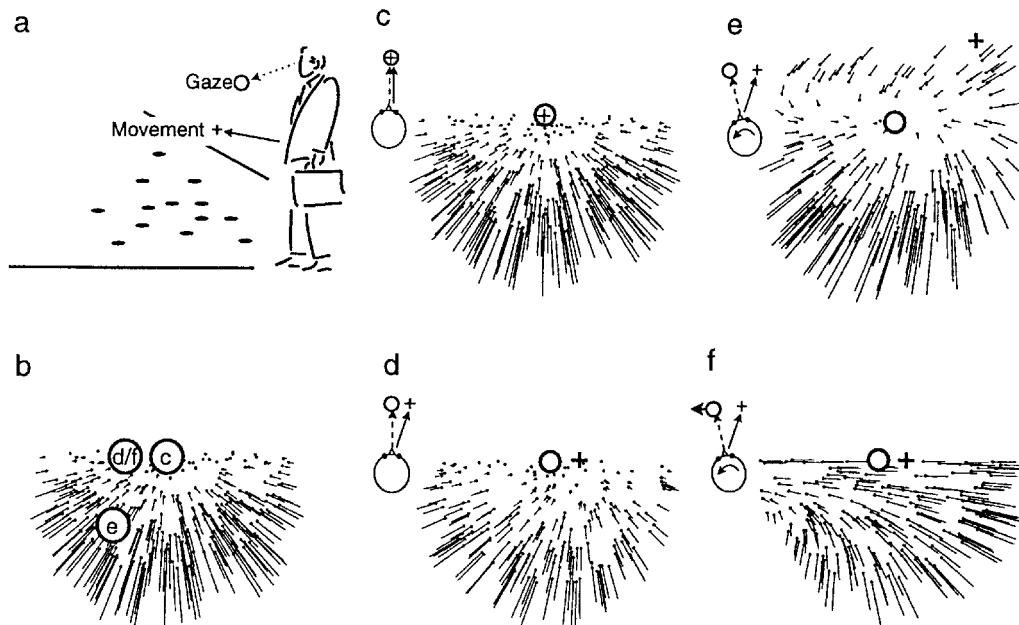


Fig. 1 a-f. Various examples of the dependence of the retinal flow field of a moving observer on gaze directions and eye movements. The observer moves on top of a ground plane. Direction of heading is indicated by a plus sign, direction of gaze by a circle

movement is what the visual system has to figure out. Figure 1b depicts the flow field in a body-centered coordinate system equivalent to the optic array in Gibson's terminology. All motion is directed away from the focus of expansion that coincides with the direction of heading. When this flow field gets projected onto the retina, the projection depends on the direction of gaze. Three gaze points indicated by circles in Fig. 1b will serve for the following retinal flow examples.

Figure 1c shows the retinal flow when the direction of gaze and the direction of movement coincide, i.e., when the observer looks straight ahead into the direction of movement. In this case the focus of expansion is visible and centered on the retina. In Fig. 1d the observer looks in a direction distinct from the direction of movement. Gazing at some fixed point on the horizon allows him to keep his eyes stationary, i.e., no eye movements occur. Again, the focus of expansion is visible, but now it is displaced from the center of the visual field. Still, it immediately indicates the direction of heading.

Figure 1e shows a situation in which the observer's gaze is directed not at the horizon but at a some element of the ground plane located below the horizon. For illustrative purposes, this element is marked by an 'e' in Fig. 1b. There are two consequences of this change in gaze direction. The first one is related to eye position (as in Fig. 1d), the second to eye velocity. The immediate effect of a change of eye position on the retinal flow field is an opposite displacement of the retinal image. The horizon has moved up in the visual field. The second, more

important difference is that, unlike the case of Fig. 1d, the point at which gaze is directed is now in motion. To stabilize the image of that point on the fovea would thus require some kind of tracking eye movement. In case the observer wants to actively track this point, he would perform a voluntary smooth pursuit in the direction of the motion of the foveated target. However, large field visual motion experienced during self-motion by itself induces reflectory eye movements for the stabilization of gaze of the optokinetic nystagmus type, accompanied by a linear vestibuloocular reflex (Miles and Busetini 1992). However, optic flow fields stimulate different parts of the retina with different directions of motion. Since optokinetic responses in foveated animals show greater sensitivity of the fovea than of the periphery, one might assume that the optokinetic eye movement is also linked to that part of optic flow that falls on the fovea. Indeed, observations in monkeys (Pekel et al. 1995) and humans have shown that optic flow fields can induce nystagmic eye movements. The direction of these eye movements closely follows the foveal motion direction, similar to the case of voluntary pursuit. Both eye movements try to null foveal flow. Thus, in both cases, the direction and speed of the eye movement are related to the observer's movement. Since direction is determined by the direction of the flow on the fovea, it is always directed away from the retinal projection of the direction of heading. Eye speed, however, might be less well-defined, depending on the gain of the eye movement.

As a consequence of eye movement, the retinal flow becomes confounded and the focus of expansion becomes obscured. The result somewhat resembles a distorted spiraling motion around the fovea (Fig. 1e). This flow field also contains a singular point. Yet this singular point is different from a focus of expansion and related to the stabilizing eye movement. Perfect stabilization of gaze (unity gain) would result in a singular point located exactly on the fovea. The visual system might capitalize on the resulting restrictions on the structure of the retinal flow in this situation (Lappe and Rauschecker 1995).

Eye movements completely unrelated to the observer's movement might also occur. The optokinetic and vestibuloocular reflexes can be suppressed during smooth pursuit of a moving target. In Fig. 1f the observer again directs his gaze to the horizon as in Fig. 1d. Yet here it is assumed that he performs a smooth eye movement in order to track an object that moves leftward along the horizon, independent of the observer's movement. In this case, the retinal flow has a very different structure, resembling a curved movement. No singular point is visible. In summary, the visual signal available to a moving observer can change fundamentally during eye movements although self-motion remains unchanged.

Humans Can Use Optic Flow for Self-Motion Estimation

What cues does the visual system use to determine self-motion from retinal flow fields in the presence of eye movements? Undoubtedly, extraretinal information is

used to cope with the visual effects of eye movements. In most studies that compared judgements of the direction of heading from optic flow in the presence and absence of extraretinal input, performance was better when extraretinal input was available (Banks et al. 1996; Royden et al. 1994; van den Berg 1992; Warren and Hannon 1990). But several of these studies have also shown that humans are quite successful even in the absence of extraretinal information, thus using only visual cues. Human subjects are highly accurate in locating the focus of expansion, in flow fields such as Fig. 1b and Fig. 1c. Errors range from less than 1° to 2.3° of visual angle, depending on the eccentricity of the focus of expansion (Warren and Kurtz 1992). In this situation, the primary cue is the radial arrangement of the motion vectors around the focus of expansion, while the distribution of flow field speeds (motion parallax) is less relevant (Warren et al. 1991).

When pursuit eye movements are performed during the presentation of optic flow stimuli, performance is similarly accurate (Royden et al. 1994; Warren and Hannon 1990). Extraretinal input can be removed by requiring subjects to fixate and then simulate eye movements along with observer movement. In this case, the results obtained in different studies were mixed. Warren and Hannon (1990) found good performance in many experimental conditions, but with an exception in the absence of motion parallax. These findings were challenged by Royden et al. (1994). Using a stimulus as in Fig. 1f, they claimed that the purely visual estimation of the direction of heading can only be performed for very slow simulated eye movements. At eye speeds greater than $1^\circ/s$ extraretinal information would be required. However, eye speed proved not to be the essential parameter. Van den Berg (1992, 1993) found good performance with simulated eye speeds up to $6^\circ/s$ using a stimulus as in Fig. 1e. More likely, the difficulties observed with the flow field in Fig. 1f arise from its difference in structure from the other flow fields (Lappe and Rauschecker 1995) and its resemblance to a flow field produced by movement on a curved path (Royden 1994).

The results can thus be summarized as follows: The human visual system is able to accurately determine the direction of heading from retinal flow fields. Extraretinal signals are often not required, but usually improve performance. In situations in which the flow field is inherently ambiguous, extraretinal information can disambiguate the visual signal.

What Neural Mechanisms Support the Visual Estimation of Heading in Primate Cortex?

Gibson's original suggestion that the pattern of motion vectors determines the direction of heading does not specify any concrete method or procedure. A large number of computational schemes have been suggested since, but only few would be considered relevant from a neurobiological point of view. One of the most

influential ideas was presented by Koenderink and van Doorn (1976), who observed that mathematically any flow field can be locally approximated by a set of four differential invariants: divergence, curl, and two components of deformation. This has led many neurophysiological studies on optic flow to use these basic components as stimuli in order to specify neuronal properties of optic flow processing.

Middle temporal Area Computes the Flow Field

The question of the cortical mechanisms of optic flow processing naturally has to start with the determination of the flow field from the retinal afferents. In the cerebral cortex of the monkey, the processing of visual motion is attributed to a successive series of areas within the dorsal stream, which is believed to be specialized in the analysis of motion and spatial relationships (Mishkin et al. 1983). Motion information proceeds from the primary visual cortex (V1) to the middle temporal area (MT) and the medial superior temporal area (MST) and from there to several higher areas in the parietal cortex (see for example Distler et al. (1993) for a recent schematic summary).

Area MT is the first area in the visual cortex that is dedicated specifically to the processing of motion. First of all, it contains a high proportion of direction selective neurons (Maunsell and Van Essen 1993). Furthermore, it has been linked to behavioral responses to motion stimuli in lesion (Newsome and Pare 1988) and microstimulation (Salzman et al. 1990) studies. The restricted size of the receptive fields in area MT would not allow individual MT neurons to perform a global analysis of the optic flow field. Rather, the properties of MT neurons are well suited for establishing a cortical representation of the retinal flow field, solving problems occurring in early estimation of visual motion (Adelson and Bergen 1985; Hildreth and Koch 1987; Movshon et al. 1985).

When the global organization of the representation of motion in the visual field in MT is considered, a relation to optic flow is already apparent. Preferred speeds increase with eccentricity (Maunsell and Van Essen 1983) similar to the way optic flow speeds naturally do. Moreover, in the peripheral visual field representation in area MT the number of direction sensitive neurons preferring motion away from the fovea is significantly higher than the number of neurons preferring motion towards the fovea (Albright 1989), a property well suited for the centrifugal structure of the flow field under natural self-motion conditions (Lappe and Rauschecker 1995).

Cells in Area MST Respond to Optic Flow Patterns

Area MST was deemed a likelier candidate for global analysis of optic flow fields because of its much larger receptive fields (Desimone and Ungerleider 1986). Early studies could occasionally identify neurons in the superior temporal sulcus that responded selectively to rotational motion, either in the frontoparallel plane or in depth, or to optical expansions (Bruce et al. 1981; Saito et al. 1986; Sakata et al. 1986). Tanaka and Saito (1989a,b) were the first to systematically investigate the response properties of MST neurons to random dot optic flow patterns. They used a set of stimuli that contained unidirectional motion, rotation, expansion, and contraction. For each of these elementary flow fields, they found neurons that responded selectively to only a single one. The selective responses of these neurons depended mainly on the spatial arrangement of motion vectors and on the size of the stimulated area. Other parameters such as shape and size of the individual motion elements, contrast, or speed gradients did not have much influence on neuronal responses.

One major concern of Tanaka and Saito was to differentiate genuine optic flow selectivity from allegedly different simple direction selectivity. This is a difficult problem, since an absolute criterion for a distinction cannot be easily formulated. In order to guarantee that some neurons possess a genuine selectivity for pattern motion (expansion, contraction, rotation) Tanaka and Saito required a neuron to be completely unselective for unidirectional motion. Only then would it be classified as expansion/contraction or rotation selective. While this is certainly a criterion to differentiate pattern motion selectivity from direction selectivity it discounted a large proportion of neurons in MST. Direction selectivity is a fundamental property of MST neurons that has led to the physiological characterization and determination of this area in the first place.

The need to differentiate optic flow processing and directional selectivity was also felt by Orban and coworkers (Lagae et al. 1994; Orban et al. 1992). They suggested a criterion based on the following assumption: Suppose a neuron has a receptive field or an area within its receptive field containing exclusive selectivity for unidirectional motion towards the right. A rotational optic flow pattern is presented to the neuron. When the center of rotation is located below the receptive field, clockwise rotation will result at first approximation in unidirectional motion towards the right in the neuron's receptive field. Counterclockwise rotation will result in leftward motion in the neuron's receptive field. If this neuron responds during clockwise but not during counterclockwise rotation, its response might be due to its direction selectivity. Now suppose that the center of rotation is moved to a position above the receptive field of the neuron. Clockwise rotation will now result in leftward, counterclockwise rotation in rightward motion in the receptive field. Then, if the neuron favors counterclockwise rotation, its response is again consistent with its direction selectivity. If, however, the neuron would respond to

clockwise rotations in both positions, then another mechanism than simple directional selectivity would be required.

Elaborate application of this procedure indeed yielded a proportion of MST neurons fulfilling this position invariance criterion, whereas cells in area MT, although responsive to optic flow components, did not (Graziano et al. 1994; Lagae et al. 1994; Orban et al. 1992). However, there are problems with this criterion, too. First of all, complete invariance towards the visual field position of an expansion stimulus would render such a neuron probably useless for a task such as heading detection, in which the position of the focus of expansion can be one of the major sources of information (Graziano et al. 1994). However, this argument would only apply to neurons that respond with exactly equal firing rates at different stimulus positions, and not if some orderly variation occurs. Second, while it is obvious that simple direction selective neurons could not pass the position invariance test, the reverse assumption, namely, that failing the position invariance test discounts a neuron from being optic flow selective, is not valid. In fact, computational considerations have shown that reversals of selectivity can be quite consistent with neuronal specification for optic flow analysis (Lappe and Rauschecker 1993a,b). Thus, the position invariance criterion is also an ad hoc requirement that would be sufficient but not necessary. The conclusions so far are mixed. There are neurons in area MST that genuinely respond to optic flow stimuli, but whether or not these neurons form a separate subpopulation differing from other MST neurons is not clear.

A more wholistic account of the complexity of optic flow sensitivity in MST was presented by Duffy and Wurtz (1991a,b), who found that the majority of MST neurons responded to several different stimuli. They suggested a classification of neurons according to the number of different flow components they respond to. Triple component neurons respond simultaneously to unidirectional motion in a preferred direction, rotation in one of the two principle directions (clockwise, counterclockwise), and either expansion or contraction. Double component cells respond to unidirectional motion and to either rotation or expansion/contraction. These two classes made up the majority of cells. Very few neurons respond to rotation and expansion/contraction but lack direction selectivity. The most selective, but least populous group consisted of single component neurons that responded only to one of the stimuli: 9% of all neurons to respond expansion or contraction, 4% to rotation. However, Duffy and Wurtz also immediately stressed that this was a rather arbitrary classification. The neuronal responses instead represented a continuum of selectivities covering not only these classes but also all stages in between.

This raises the question of whether neurons in MST perform a mathematical decomposition of the flow field into a set of basic components such as expansion and rotation. Several lines of evidence in addition to the observations of Duffy and Wurtz suggest that this is not the case. A cell that extracts expansion (divergence) from an optic flow stimulus in a mathematical sense would have to respond with equal activity to pure expansion and to a stimulus where the same

expansion is disturbed by adding some other flow component, for instance rotation. This is not true for MST cells (Graziano et al. 1994; Orban et al. 1992). Instead, some MST cells even prefer vectorial combinations of rotation and expansion/contraction over the two individual flow patterns and display a selectivity for spiral motion (Graziano et al. 1994). Furthermore, for a complete mathematical decomposition, two components of deformation are necessary in addition to divergence (expansion/contraction) and curl (rotation) (Koenderink and van Doorn 1976). Cells responding exclusively to deformation were practically absent in MST (Lagae et al. 1994). There also are theoretical considerations reminding us to consider the decomposition into basic flow components with care. Decomposition is a local linearization of the flow field (Koenderink and van Doorn 1976). This means that mathematically at any point in a dense flow field, decomposition is valid only within a small vicinity of that point. This creates two problems with respect to the properties of MST neurons. First, the receptive fields are too large to perform a local analysis. Second, the observed position invariance would render a proposed attribution of the response to a localized position in the visual field inappropriate.

In summary, these results suggest that MST does not use a set of channels selective for just expansion, contraction and rotation, but rather a graded continuum of response properties in which single neurons might respond to several different flow components and to combinations of them.

Can Area MST Compute Self-Motion?

How else, then, would self-motion be represented or computed in MST? A mechanism well established for other complex brain functions is the distributed encoding of external, behavior-relevant parameters by whole populations of neurons (Andersen et al. 1993; Georgopoulos et al. 1986; Lee et al. 1988; Van Gisbergen et al. 1987). In this view, the representation of self-motion would be assumed to be spread across a large number of neurons in MST. Each individual neuron would make only a small contribution to the global self-motion representation by modulating its response strength depending on whether the flow field input is consistent with a preferred self-motion. A computational model of such a distributed representation of self-motion has been proposed by Lappe and Rauschecker (1993b). This model implements a minimization procedure for visual heading detection in two layers of neuron-like elements. The first layer contains a representation of the flow field modeled on area MT. The second layer contains cells that individually test the compatibility of their flow field input with a certain direction of heading. The overall direction of heading specified by the input flow field is finally computed by the full population of second layer neurons. This model predicts a computational map of heading directions in area MST. This map could either be represented implicitly by the population, or alternatively read out

by a set of dedicated neurons either within area MST or in subsequent brain areas that require self-motion information.

When it comes to the question of whether optic flow sensitive neurons in MST possess the capability to estimate self-motion from optic flow fields, there are two problems with the paradigms used in most studies. The first concerns the size of the stimuli. During self-motion, optic flow normally covers the full visual field of the observer, and the global structure of the flow is of importance. The second problem concerns the placement of the stimuli. An important parameter for the determination of heading in the absence of eye movements is the position of the focus of expansion in the visual field. However, most studies in area MST that tested the positional modulation of optic flow responses used small stimuli (diameters ranging from 10° in Lagae et al. 1994 to 20° in Graziano et al. 1994 and 33° in Duffy and Wurtz 1991b), placed the stimuli with respect to the receptive field of the neuron (with the exception of Duffy and Wurtz 1991b), and tested positional variation by moving the full stimulus instead of only the singular point. These tests are adequate for the basic response properties of individual neurons. However, they confound stimulus extent in the visual field with position of the focus of expansion.

To test a possible relation of the neuronal response properties to self-motion, a variation of the location of the singular point in full-field stimuli would be more suitable. This has been acknowledged only recently (Duffy and Wurtz 1995; Pekel et al. 1996). Lappe et al. (1996) recently presented experiments explicitly carried out in analogy to computer simulations of model neurons. In these experiments, a monkey was required to fixate a central spot of light on a projection screen. Full-field (90° by 90°) computer generated optic flow stimuli simulating approaching (expansion) and subsequently receding (contraction) self-motion with respect to a random cloud of dots in three-dimensional space were projected. They displayed entirely realistic self-motion flow fields. Dots accelerated with eccentricity, grew larger in size as they approached the monkey, and moved with motion parallax according to their distance in depth. To determine the dependence of neuronal responses on the singular point in the optic flow stimulus, 17 different movie sequences were used. In each of these sequences the singular point was located in a different position, either in the center of the screen, or at one of 16 peripheral locations.

The responses of a single exemplary neuron are shown in Fig. 2a,b. The modulations of response strength with the position of the singular point on the projection screen are displayed by three-dimensional surface plots. In these plots, the (x,y)-plane represents the positions of the singular point on the screen, while the z-axis indicates the response rate in spikes per second. The neuronal responses to expansion (a) and contraction (b) vary smoothly with the position of the singular point. Such a sigmoidal response profile is observed in many MST neurons (see also Duffy and Wurtz 1995, their Fig. 13B). Responses to both expansion and contraction can be elicited by proper placement of the singular point. Therefore, the neuron's response is not position invariant when the singular

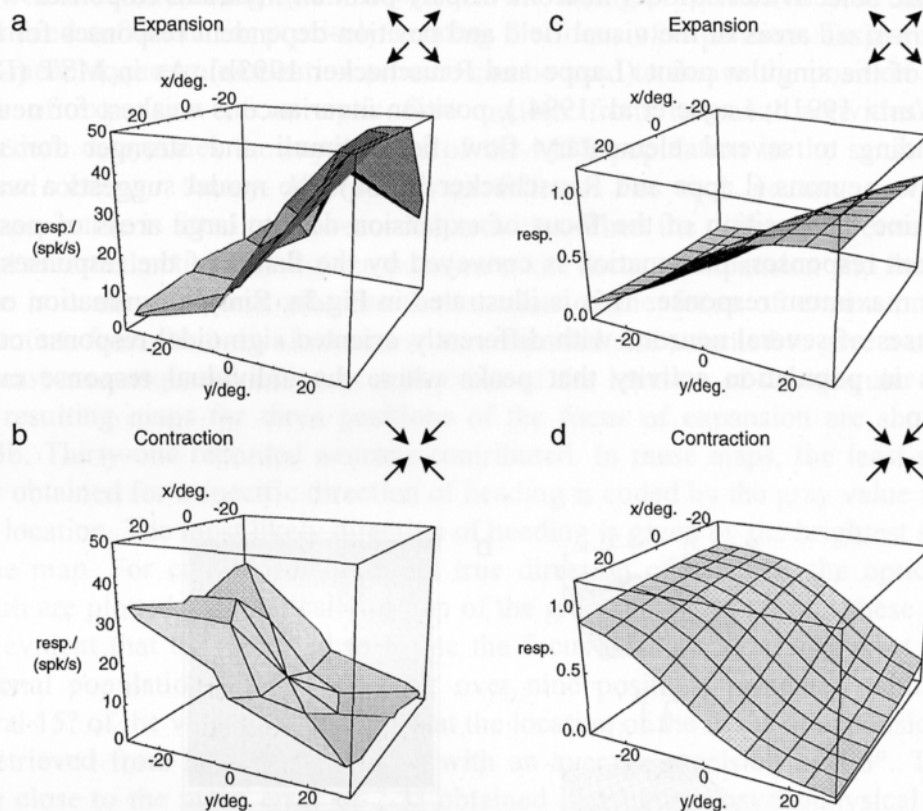


Fig. 2 a-d. Single-neuron activity as a function of the position of the focus of expansion/contraction in the visual field. *Left:* Data from a recording in area MST of an awake macaque monkey. *Right:* Computer simulation of a single neuron from the model of Lappe and Rauschecker (1993b)

point is moved over the full visual field. However, if the singular point were to be moved within a restricted area of the size used in most previous studies, the observed responses could be restricted to only one stimulus type. For instance, in all of the lower hemifield ($y < 0$, left half of the diagrams), the neuron responds exclusively to contraction.

These experimental findings can also be recreated in computer simulations of the model of Lappe and Rauschecker (1993b). The characteristics of a single model neuron (Fig. 2c,d) are quite similar to the recorded data in Fig. 2a,b with respect to the sigmoidal shape of response modulation. In simulations, it has been found that single neurons in this model can capture a wide range of the properties of MST neurons. Single model neurons can respond to unidirectional translation, expansion/contraction, and rotation rather like triple component cells in area MST (Lappe and Rauschecker 1993b). They might also respond to only a subset of these stimuli (Lappe and Rauschecker 1993a) or to linear combinations (spiral patterns). Thus, the model successfully captures the observed continuum of

response selectivities. Model neurons display position invariant responses within medium-sized areas of the visual field and position-dependent responses for large shifts of the singular point (Lappe and Rauschecker 1993b). As in MST (Duffy and Wurtz 1991b; Lagae et al. 1994), position invariance is weakest for neurons responding to several elementary flow field stimuli and stronger for more selective neurons (Lappe and Rauschecker 1993a). The model suggests a way to determine the position of the focus of expansion despite large areas of position invariant responses. Information is conveyed by the flanks of the responses, not by the maximum response. This is illustrated in Fig.3a. Simple summation of the responses of several neurons with differently oriented sigmoidal response curves results in population activity that peaks where the individual response curves overlap.

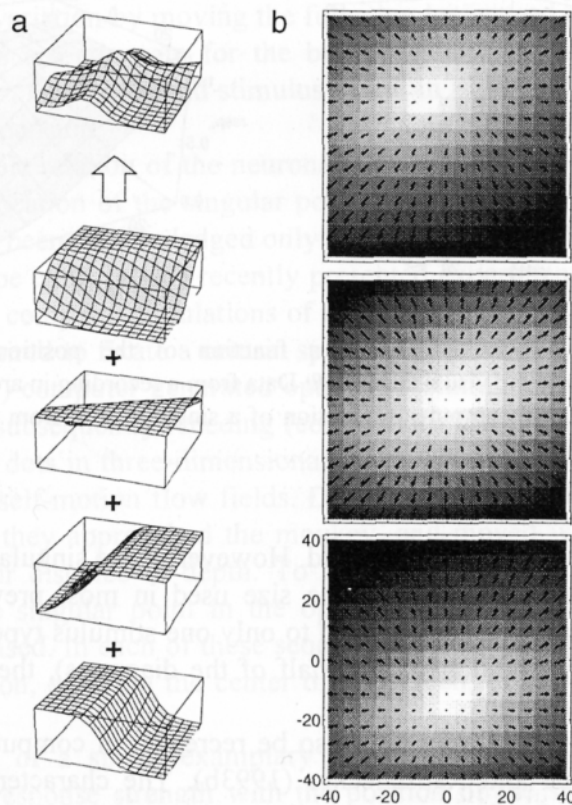


Fig. 3 a,b. Population encoding of the direction of heading. *Left:* Schematic illustration showing how sigmoidal response curves of individual neurons can be combined to give a maximum in population activity. *Right:* Grayscale maps indicating the location of the focus of expansion as retrieved from the recorded neuronal activities of 31 MST cells for three different true locations. Flow stimuli are shown superimposed

It would be interesting to know whether the tuning properties of MST neurons are indeed sufficient for precisely locating the focus of expansion. To test this, a least-mean-square minimization scheme can be used to derive the position of the focus of expansion of an optic flow pattern from neuronal activities. This procedure determines the capabilities of the MST population in the sense of an optimal observer theory. It proceeds as follows. For each neuron, a sigmoid response curve is fitted to the recorded activities. Then the difference between the actual recorded activity of a given position of the focus of expansion and the fitted curve is used as a constraint for the location of the focus of expansion. The constraints from the individual neurons are squared and summed to give a map of the least-mean-squared errors as a function of the location of the singular point. The resulting maps for three positions of the focus of expansion are shown in Fig. 3b. Thirty-one recorded neurons contributed. In these maps, the least-square error obtained for a specific direction of heading is coded by the gray value at that map location. The most likely direction of heading is given by the brightest square in the map. For comparison with the true direction of heading, the optic flow stimuli are plotted schematically on top of the gray-scale maps. From these maps, it is evident that the potential to locate the focus of expansion is present in the neuronal population. The mean error over nine positions presented within the central 15° of the visual field shows that the location of the focus of expansion can be retrieved from neuronal activities with an average precision of 4.3° . This is quite close to the mean error of 2.3° obtained in a human psychophysical study with comparable stimuli (Warren and Kurtz 1992).

Some MST neurons have a peak-shaped response dependence on the position of the singular point rather than a sigmoidal one (Duffy and Wurtz 1995). These neurons might individually prefer a single direction of heading. A hypothesis already put forward by Lappe and Rauschecker (1993b) proposes that such neurons might already read out the activity of MST subpopulations provided by the more basic sigmoidal shaped response curves. The response properties of these neurons would then be similar to the top panel in Fig. 3a.

Eye Movements

Areas MT and MST are related to eye movements in several ways. Both areas are involved in the generation of smooth pursuit and optokinetic eye movements (Erickson and Dow 1989; Kawano et al. 1994; Komatsu and Wurtz 1988a). Lesions in MT/MST produce pursuit and optokinetic deficits (Dürsteler and Wurtz 1988). A subset of MT neurons selectively projects to subcortical structures that control optokinetic eye movements (Hoffmann et al. 1992; Ilg and Hoffmann 1993).

But area MST also contains information about the occurrence of eye movement. A subpopulation of MST neurons discharges during ongoing smooth pursuit eye

movements (Erickson and Dow 1989; Komatsu and Wurtz 1988a). Part of the response of these neurons originates from the visual signal induced by eye movement, but some neurons retain their firing rate even in the absence of visual stimulation (Newsome et al. 1988).

Other MST cells show a striking ability to distinguish between active, eye movement-induced motion and passive, externally-induced object motion (Erickson and Thier 1991). This behavior was found in experiments using a paradigm quite similar to that used in psychophysical investigations of extraretinal signals in heading detection. Erickson and Thier compared two situations with identical visual, but differing extraretinal input. In the passive condition, a moving bar was swept across the receptive field of a neuron, while the monkey was required to keep its eyes stationary. In the active condition, the bar was stationary on the screen, and the monkey actively performed an eye movement that induced identical visual movement of the bar on the retina. Some neurons responded preferentially in the passive condition, thus revealing selectivity only to motion in the real world. Just as the extraretinal input to the pursuit neurons (Newsome et al. 1988) this phenomenon was not found earlier in the visual motion pathway, neither in area MT (Erickson and Thier 1991), nor in area V1 (Ilg and Thier 1996).

Could these extraretinal signals be useful for self-motion detection? A dependence of some of the optic flow processing MST neurons on pursuit signals has been reported by Duffy and Wurtz (1994). Lappe et al. (1994) have argued that pursuit neurons in MST could provide a signal of present eye velocity that might allow optic flow processing neurons to compensate to some degree for the visual effects of this eye movement. In this model, the pursuit signal is used to subtract a purely eye movement induced flow field component from the full retinal flow. However, this process is likely to be incomplete. For instance, the speed of eye movement seems to be less well represented by the pursuit neurons than its direction. Precise heading detection thus would still have to rely heavily on the visual signal, which would be merely augmented by extraretinal compensation. Such a hybrid model can account for the most prevalent conditions in which human heading detection has been shown to rely on extraretinal input, and it also leads to neurons that implement the active/passive distinction observed in MST (Lappe et al. 1994).

If optic flow processing neurons use pursuit signals in such a way, it should be reflected by neural responses to optic flow stimuli during ongoing pursuit eye movement. Model simulations predict that the responses to optic flow stimuli presented in the screen center are altered in a direction dependent manner during pursuit. Figure 4a,b shows the results of such a simulation. A neuron was probed with flow field stimuli displaying a centered expansion or contraction, accompanied by simulated rotations in different directions and an extraretinal signal either switched on or off. The circle indicates the response to the flow stimulus alone. The dark bar shows the responses during additional simulated eye

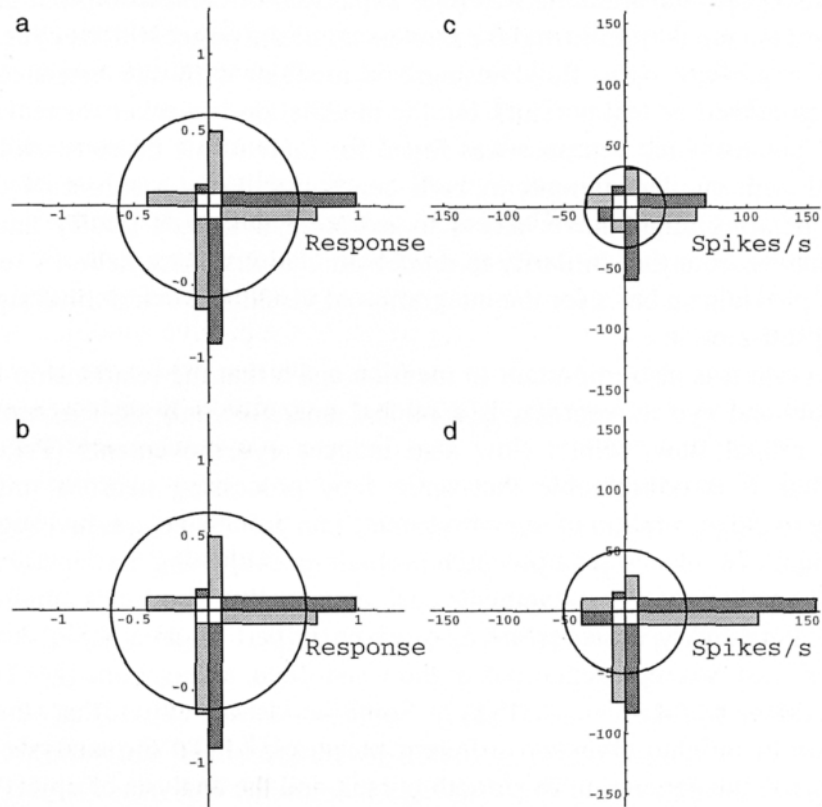


Fig. 4 a-d. Directional modulation of optic flow responses by real (light bars) or simulated (dark bars) pursuit eye movements. The polar plots show the neuronal response strengths for eye movements in four directions. *Left:* Model prediction. *Right:* Data from a single-neuron recording

movements in the four cardinal directions. The light bar shows the responses when an extraretinal signal allows partial remedy of eye movement effects. For both flow stimuli, the response is altered by the addition of eye rotation in the same way. Simulated downward pursuit enhances the response; simulated upward pursuit leads to a response weaker than the response to pure optic flow. In the presence of a simulated extraretinal signal, response modulation is diminished, and the response becomes more similar to the pure optic flow response.

When the same paradigm is employed in single unit recordings in monkey area MST, some neurons show similar behavior. An example of the responses of a single neuron is shown in Fig. 4c,d. The experiment compared three different conditions. In the first condition (eye stationary, circle) the monkey fixated a stationary target and was presented with an expanding or contracting optic flow stimulus. In the second condition (simulated pursuit, dark bars) the monkey again fixated a stationary target, but the stimulus contained expansion/contraction superimposed with a rotation around one of four axes. In the third condition (real

pursuit, light bars) the stimulus was pure expansion or contraction, but the target moved, and the monkey followed the movement of the target with its eyes. For the neuron in Fig. 4c,d, optic flow response is modulated by the presence of eye rotation (simulated or real pursuit), but the modulation is weaker for real than for simulated pursuit. Such behavior was found for some of the neurons while others responded with similar strength in both conditions. Only a subset of the flow sensitive neurons might have access to extraretinal signals (Duffy and Wurtz 1994). Judging from the similarity to model simulations, these neurons seem well suited for providing a basis for the integration of visual and extraretinal signals for analyzing self-motion.

At this point it is also important to mention again that the relationship between retinal flow and eye movements is a mutual one. Not only do eye movements influence retinal flow, retinal flow also induces eye movements (Pekel et al. 1995). Thus it is conceivable that optic flow processing neurons might also contribute to the generation of eye movements in a process not yet investigated.

This might help in solving a potential problem in evaluating the function of area MST, since voluntary eye movements such as smooth pursuit of a small moving object by a stationary observer are also driven in part by area MST. Area MST contains at least two representations of the visual field, a dorsal one (MSTd) and a ventrolateral one (MSTl or MSTv). Some evidence exists that these two representations might serve two different purposes, MSTd the analysis of self-motion, MSTl the generation of smooth pursuit and the analysis of object motion. The original report of Tanaka and Saito (1989a) found expansion, contraction, and rotation cells to be clustered within the dorsal part of MST. In contrast, many cells in the ventrolateral part of MST respond well to small moving stimuli or to differential motion between a small point and a large background (Komatsu and Wurtz 1988b; Tanaka et al. 1993). Such a response would be appropriate for the control of pursuit eye movements and the analysis of object motion. However, there are some problems with such a strict differentiation. Neuronal response properties in MSTl are quite heterogeneous in several aspects. A sizable portion of the MSTl cell population prefers large stimuli instead of small spots and their visual and pursuit related functions resemble those of cells in MSTd (Komatsu and Wurtz 1988a,b). This is also true for extraretinal influences (Erickson and Thier 1991; Newsome et al. 1988) and for visual responses related to ocular following and optokinetic nystagmus (Kawano et al. 1994). Responses to optic flow stimuli have also been reported outside MSTd near or in the fundus of the superior temporal sulcus (Lagae et al. 1994; Pekel et al. 1996). Also, Tanaka and Saito (1989a) as well as Tanaka et al. (1993) found optic flow selective cells in the ventrolateral part of MST, albeit in a much smaller percentage than in MSTd. On the other hand, Graziano et al. (1994) showed that neurons in MSTd respond well to small optic flow stimuli. They suggested that such neurons could also contribute to the analysis of object motion. However, the preferred stimulus size might not be a decisive criterion for distinguishing between object- and self-motion, since psychophysical effects clearly related to self-motion can also be

observed with rather small optic flow stimuli (Andersen and Braunstein 1985; Warren and Kurtz 1992). In summary, the dorsal part of MST seems to be devoted mainly to the processing of self-motion and possibly to the analysis of the visual consequences of eye movements in this task. The ventrolateral part is more heterogeneous and contains cells involved in the generation and maintenance of eye movements. However, since any self-motion immediately poses a challenge to the stability of the retinal image or at least to parts of it, the finding that neuronal functions of self-motion processing and of eye movement generation are located in immediate vicinity in the cerebral cortex should come as no surprise.

Multimodal Representation of Self-Motion

For a full representation of self-motion, other sensory signals need to be incorporated, and the derived self-motion parameters finally need to be represented in a reference frame suitable to controlling body movements (Telford et al. 1995). One signal, which only recently came to be appreciated for its supporting role in heading detection, is retinal disparity. In principle, since optic flow depends on the depth structure of the visual environment, depth cues obtained from retinal disparities can be helpful in determination of the direction of heading. However, a role of stereo vision in heading detection has usually been dismissed on the grounds that disparity only operates successfully in near vision while heading detection is essentially a far-vision process. Only recently it was shown that humans can use depth cues derived from retinal disparities to improve their performance in noisy flow fields (van den Berg and Brenner 1994).

Like cells in many other visual areas, MST cells carry a disparity signal. However, some neurons in area MST show a distinct disparity dependence that suggests that stereoscopic depth is integrated with visual motion in a manner suitable for self-motion analysis. These neurons reverse their preferred direction depending on whether unidirectional motion is presented in a plane nearer or farther than fixation distance (Roy and Wurtz 1992). Such an arrangement of motion directions is experienced during self motion when one fixates a stationary object towards the side of the movement path.

Also, vestibular and proprioceptive signals might contribute to heading detection. However, their primary value lies in the transformation of visually determined heading into a representation suitable to controlling body movements (Telford et al. 1995). A vestibular input to the pursuit neurons in MST is organized to signal the direction of combined eye and head movements (Thier and Erickson 1992). Also, eye-position-dependent modulation of neuronal responses in MST (Bremmer et al., in press) might be used to shift from a retinal to a head centered coordinate system using a mechanism proposed for other parietal areas (Andersen et al. 1993). Evidence that area MST is indeed involved in the visual control of body movements was obtained in a recent lesion study (Duffy and

Wurtz 1996). Lesions of area MST resulted in postural instabilities and disruption of the ability to perform postural responses to optic flow stimuli.

There is also some recent evidence that another area in parietal cortex, namely, the ventral intraparietal (VIP) area, might be involved in self-motion processing from multiple sensory input. Activity during optic flow stimulation was recorded not only in areas MT and MST but also in a region corresponding to area VIP. In physiological experiments by Bremmer et al. (this volume), neurons in area VIP were shown to respond to optic flow stimuli, but also to vestibular stimulation and during eye movements.

Thus, it is fair to conclude that many sensory signals arising during self-motion converge in parietal cortex. The visual determination of heading most likely takes place in area MST. However, from the data available so far, it seems too early to conclude how and in which particular area the multiple signals supporting self-motion analysis are transformed into a representation of body motion in space.

Conclusion

From the described physiological, psychophysical, and computational studies, a unified account of self-motion processing in the dorsal stream of the primate cortex emerges. It starts with local motion sensitive cells in primary visual cortex that are integrated in area MT to form the exquisite directional selectivity of MT neurons and compute local two-dimensional motion. Area MT contains a representation of the optic flow field that is well suited to serve as a basis for flow field analysis. Area MST uses the flow field representation provided by area MT to extract self-motion parameters. Cells responding to a variety of flow patterns could form a population encoding of the direction of heading. At the level of area MST, a number of additional signals that support heading detection are combined with visual information. These are eye movement signals, retinal disparity and, possibly, vestibular signals. The result is a multimodal, vision-dominated representation of self-motion in area MST or even higher parietal areas.

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