

Optic flow illusion and single neuron behaviour reconciled by a population model

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Abstract

Radial patterns of optic flow contain a centre of expansion that indicates the observer's direction of self-movement. When the radial pattern is viewed with transparently overlapping unidirectional motion, the centre of expansion appears to shift in the direction of the unidirectional motion [Duffy, C.J. & Wurtz, R.H. (1993) *Vision Res.*, **33**, 1481–1490]. Neurons in the medial superior temporal (MST) area of monkey cerebral cortex are thought to mediate optic flow analysis, but they do not shift their responses to parallel the illusion created by transparent overlap. The population-based model of optic flow analysis proposed by Lappe and Rauschecker replicates the illusory shift observed in perceptual studies [Lappe, M. & Rauschecker, J.P. (1995) *Vision Res.*, **35**, 1619–1631]. We analysed the behaviour of constituent neurons in the model, to gain insight into neuronal mechanisms underlying the illusion. Single model neurons did not show the illusory shift but rather graded variations of their response specificity. The shift required the aggregate response of the population. We compared the model's predictions about the behaviour of single neurons with the responses recorded from area MST. The predicted distribution of overlap effects agreed with that observed in area MST. The success of the population-based model in predicting the illusion and the neuronal behaviour suggests that area MST uses the graded responses of single neurons to create a population response that supports optic flow perception.

Introduction

The radial patterns of optic flow seen during forward self-movement present a centre of motion which can indicate the direction of heading. When radial and unidirectional motion are presented as transparently overlapping patterns, human observers perceive a shift of the radial centre of motion in the same direction as the unidirectional motion (Duffy & Wurtz, 1993). The perceptual shift is different from the displacement of the centre of motion that occurs when radial patterns of optic flow are combined with unidirectional motion by vector summation. In that case, the centre of motion in the radial pattern is shifted in the direction opposite to the unidirectional motion. Figure 1 illustrates and summarizes the perceptual shift of the centre of motion. It starts out with two random-dot optic flow patterns. The first is a radial expansion centred on the screen. The second is a unidirectional motion. In the example of Fig. 1 this motion is directed rightward. In the vector-summed condition, the individual motion vectors of the two patterns are summed vectorially. This generates a new radial expansion pattern which has its centre of motion on the left. In the transparent-overlap condition, the two motion patterns are presented simultaneously in transparent motion. The two summation conditions lead to different perceived locations of the centre of motion in human subjects (Duffy & Wurtz, 1993). In the vector-summed condition, subjects see the centre of motion at its correct position on the left. In contrast, in the transparent-overlap condition, the centre of expansion is perceived on the right, i.e. displaced in the direction of the overlapping unidirectional motion.

A similar result is obtained from a population coding model of heading detection which correctly predicts both the heading of motion in simple radial flow fields and the shift induced by transparently overlapping unidirectional motion (Lappe & Rauschecker, 1995). Figure 1B shows the output of the population heading map in this model for the two conditions. The greyscale figures display the distribution of neuronal activity in this map. In both conditions, the brightness peak, i.e. the maximum of the population activity in the model, matches the perceived location of the centre of expansion.

Neurons in the medial superior temporal (MST) area of monkey extrastriate visual cortex respond to optic flow stimuli (Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994; Lagae, Maes, Raiguel, Xiao, & Orban, 1994). When radial patterns of optic flow are combined with unidirectional motion by vector summation, the centre of motion in the radial pattern is shifted in the direction opposite to the unidirectional motion (vector-summed condition in Fig. 1). Studies of MST neurons have shown that they exhibit response selectivities for shifted centres of motion (Duffy & Wurtz, 1995; Lappe, Bremmer, Pekel, Thiele, & Hoffmann, 1996), supporting the suggestion that they are involved in the cortical analysis of optic flow. From such centre-of-motion response profiles it is possible to determine the location of the centre of expansion and hence the direction of heading by means of a population analysis (Lappe *et al.*, 1996).

If area MST is involved in the analysis of optic flow, the different percepts occurring with the combined and transparent stimuli should be reflected in some way in the neuronal responses. The centre-of-motion response profiles provide a basis for evaluating whether overlapping radial and unidirectional motion cause a shift of the preferred centre of motion that parallels the perceptual effect. What kind of neuronal behaviour

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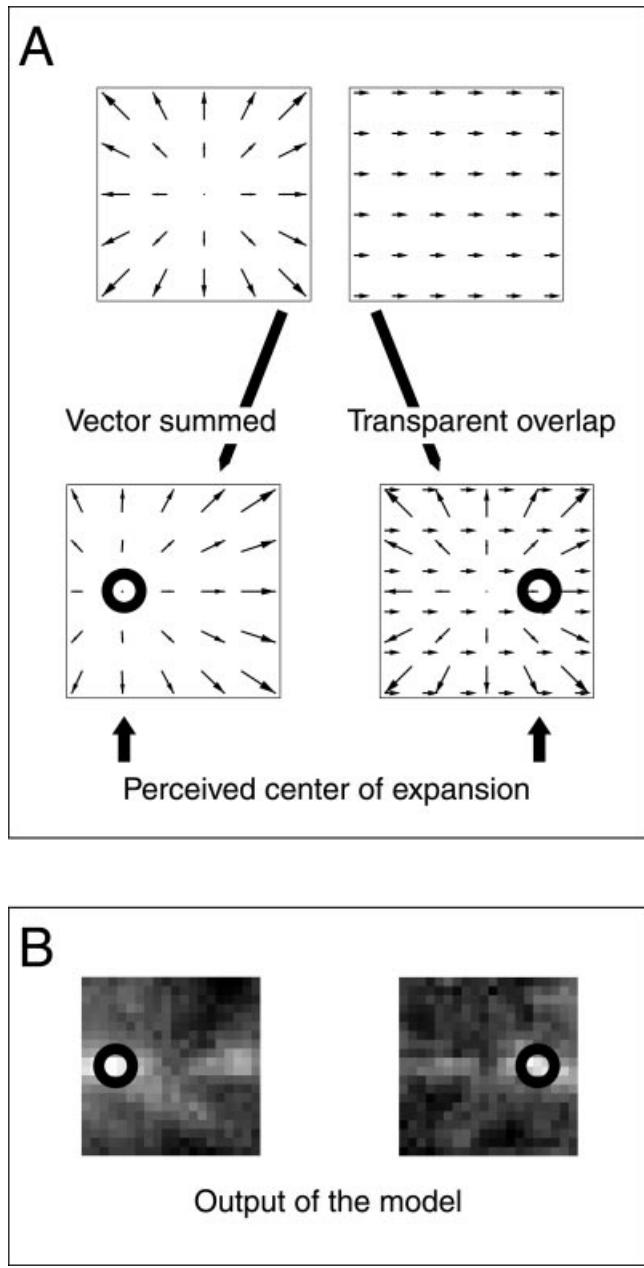


FIG. 1. Illusory transformation of optic flow fields. (A) Two random dot optic flow patterns, a radial expansion centred on the screen and a unidirectional (here rightward) motion, are joined together in either one of two ways. In the vector-summed condition, the motion vectors of the two patterns are summed vectorially. The result is a new radial expansion which is now centred on the left. In the transparent-overlap condition, both motion patterns are presented simultaneously as a transparent motion of two different patterns. When human subjects are asked to locate the centre of the radial motion in those stimuli, the responses in the two conditions differ very much (Duffy & Wurtz, 1993). For the vector-summed stimulus, subjects report the correct position on the left. For the transparent-overlap stimulus, subjects instead perceive the centre of expansion displaced towards the right, i.e. in the direction of the unidirectional motion. (B) Outputs of the population heading map in the model of Lappe & Rauschecker (1995). This model computes the direction of heading from the optic flow using populations of MST-like neurons. It proposes that heading is determined from the distribution of neuronal activity in a two-dimensional map of heading directions. The greyscale figures display this map. Each position in the map contains a population of optic flow selective neurons. The brightness of each square gives the combined activity of all neurons within such a population. In both conditions, the brightness peak, i.e. the maximum of the population activity, matches the perceived location of the centre of expansion.

might one expect? Individual neurons exhibit a preference for certain locations of the centre of expansion in radial (vector-summed) stimuli. Therefore a first hypothesis might be that their preference for the location of the centre of expansion shifts or flips when transparent stimuli are presented, much as the human perception of the centre-of-motion shifts or flips to the opposite side of the centre of the visual field in that case. As we will show below, the responses of the vast majority of MST neurons are not consistent with this simple hypothesis. We have therefore presented the vector sum and transparent-overlap stimuli to single neurons in the population-based model. The results of these simulations were used as a new prediction for the behaviour of optic flow processing neurons in response to the illusory stimuli. This analysis was compared with the result of studies of 228 MST neurons using similar stimuli. We found that the population-based model not only predicts the illusory shift of the centre of expansion, but also predicts the behaviour of individual MST neurons. Thus, we conclude that MST uses a population-encoding approach to signal the location of the centre of expansion in optic flow for the perception of heading direction during observer self-movement.

Methods

Modelling

The population-encoding model of Lappe and Rauschecker and its relationship to the neurophysiology of optic flow processing has been described in detail in Lappe & Rauschecker (1993) and Lappe *et al.* (1996). Briefly it consists of a first layer of neurons that encodes the optic flow field and a second layer of neurons that analyses the optic flow and estimates the direction of heading. The first layer models the representation of the optic flow field in the middle temporal (MT) area. It contains neurons selective for the speed and direction of local visual motion. Subpopulations of neurons with identical receptive field positions, but different motion preferences, are combined into hypercolumns. The distribution of activity in such a hypercolumn is used to encode local visual motion at the receptive field position. In the simulations, the number of hypercolumns is matched to the number of moving dots.

The second layer models optic flow processing in area MST. Each second layer neuron receives synaptic input from a random subset of 30 first-layer hypercolumns. The strengths of synaptic connections are predefined such that the network effectively implements an optimization algorithm for heading detection from optic flow (Lappe & Rauschecker, 1993). This algorithm, and its neural implementation in the model, determines the direction of heading that optimally matches the input flow field. The choice of synaptic connections in the model is thus by design and does not use a learning rule. For the scope of this paper, it is important to note that the illusory effect at no point influenced the design of the model. The model was solely devised to estimate heading. The reproduction of the illusory shift in the model is an emerging property.

The direction of heading is retrieved in the model from a population code. The second layer contains a two-dimensional map of possible heading directions in which each direction is represented by a separate population of neurons. The connections are chosen so that the summed neuronal activity in such a single population estimates the likelihood that the measured optic flow is consistent with the direction of heading of this population. The correct direction of heading is then found by comparing the activities of the different

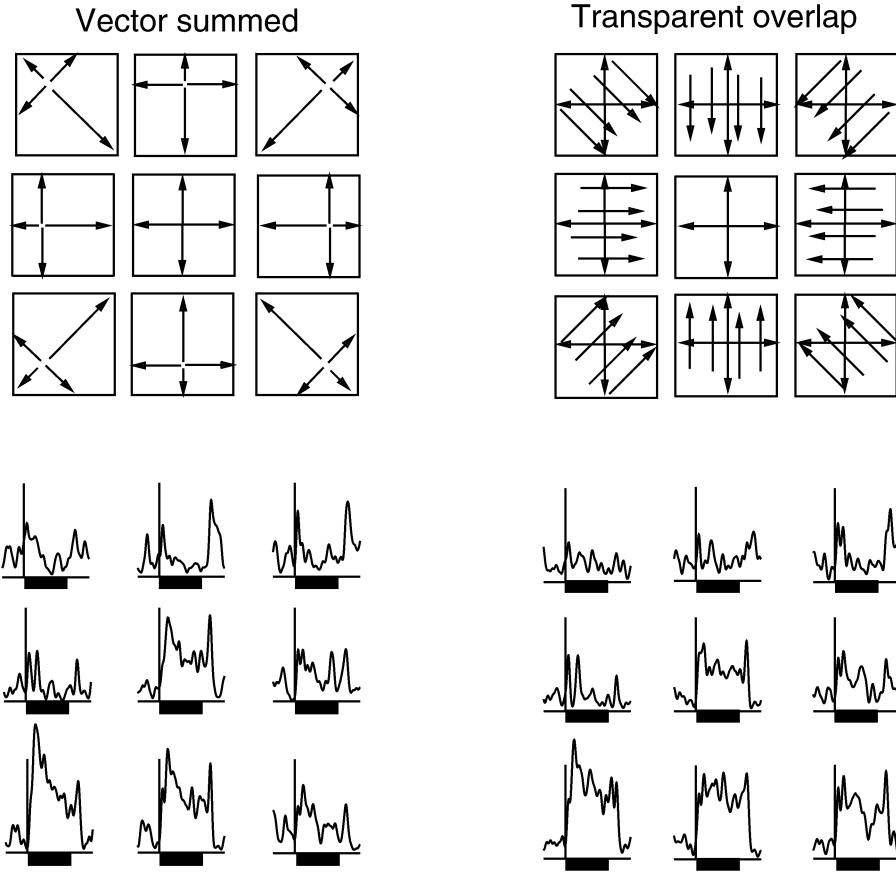


FIG. 2. Responses to vector-summed and transparent-overlap stimuli in a single MST neuron. The top panels show the two stimulus sets. Each square depicts the pattern of dot motion on the $90 \times 90^\circ$ stimulus screen. Both included pure radial motion (centre squares) as well as unidirectional motion in eight directions (surrounding squares). This uniform motion was either vector summed (left) or transparently overlapping (right). The bottom panels show spike density histograms for a single neuron giving mean responses over six presentations of each stimulus. The horizontal bar marks the 1-s stimulus period. The vertical line indicates 100 spikes/s discharge rate. The neuronal responses show little differences between the two stimulus sets. In both conditions the neuron responds best to the motions presented in the lower left stimulus squares. In both conditions, unidirectional motion was right-upward. However, the perceptual displacement of the centre of motion is in opposite directions for the two conditions. In the vector-summed condition, the location of the centre of motion is in the lower left hemifield as shown in the lower left square of the vector-summed stimuli. In the transparent-overlap condition, the centre of expansion is perceived displaced towards the upper right. Yet, the neuron's responses are very similar.

populations, i.e. finding the maximum activity in the population heading map.

The concept that the direction of heading is determined by a population of neurons, not by any single neuron alone, has important consequences for the understanding of the signal that each individual neuron transmits. The response of each individual model neuron is a sigmoid function of the position of the centre of expansion (Lappe *et al.*, 1996). However, the population signal is combined from a large number of such individual responses and therefore shows a different dependence on the location of the centre of expansion. Because the activity from individual neurons is summed to produce the population output, the population response reaches its maximum at the location of the centre of expansion, i.e. where the single neuron response curves optimally overlap. The population response has a peak-shaped dependence on the position of the centre of expansion.

Previous work has already shown that the distribution of population activity in response to the transparent stimuli is consistent with the results of the human psychophysical experiments (Lappe & Rauschecker, 1995). Here we intended to determine the responses to these transparent stimuli in single model neurons. We will compare them with the responses to combined stimuli in which the centre of expansion is displaced in the opposite direction. For these simulations, vector fields resembling the transparent and combined stimuli were constructed and were used as input to the model. Then the resulting activities of single model neurons were calculated. The parameters of the stimuli were identical to the parameters used in Duffy & Wurtz (1993, 1995). We varied the direction of the uniform motion component while keeping the radial motion component always centred in the visual field.

Experimental methods

The MST neurons included in this study are in part from the sample described in Duffy & Wurtz (1997). Detailed experimental methods can be found in that reference. Briefly, single neurons were recorded from the cortex of two adult rhesus monkeys. Fixation control was maintained using the scleral search coil technique while the monkey viewed moving dot visual displays on a $90 \times 90^\circ$ rear-projection screen. Neurons were tested with vector-sum and transparent-overlap stimuli constructed by modification of a radial expansion in the screen centre. In the vector sum stimuli, unidirectional motion in one of eight directions was vectorially combined with the centred centre of expansion radial pattern. In the transparent-overlap stimuli, the same unidirectional motion was presented transparently overlapping the centred centre of expansion radial pattern. These stimuli contained 360 dots, each subtending 0.75° in diameter. Frame rate and refresh rate of the display was 60 Hz. As the transparent-overlap stimuli had the same total number of dots, only half as many were in each of the two motion patterns.

Under general anaesthesia, scleral search coils, recording cylinders, and a head holder were implanted. All protocols were approved by the Institute Animal Care and Use Committee and in accord with Public Health Service Policy on the humane care and use of laboratory animals. Single neuron activity was recorded in both hemispheres of the two monkeys using standard techniques. Histological analysis confirmed the locations of recording sites relative to electrolytic marks and anatomical landmarks.

Each trial began with the appearance of a red fixation point 0.25° in diameter. The monkey had to establish fixation within 500 ms and keep it for a period between 6 and 7.5 s. During this time, two or three randomly selected visual motion stimuli were presented sequentially. Each lasted 1 s with an interstimulus interval of 1.5 s. Hand-held

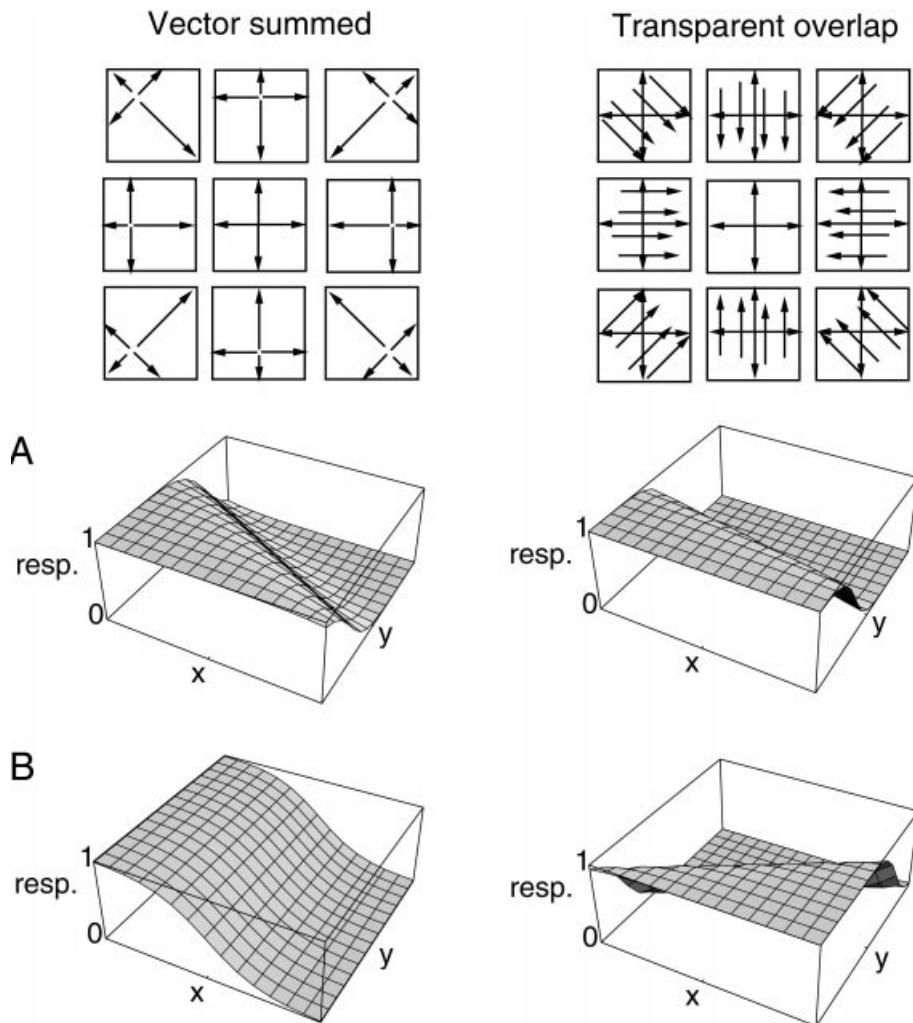


FIG. 3. Responses to vector-summed and transparent-overlap stimuli in single model neurons. Each surface plot displays the responses to one set of stimuli as a function of the horizontal (x) and vertical (y) speed of the uniform motion that was vector summed or overlapped. For the vector-summed stimuli (left), these plots are equivalent to the response profiles for the position of the centre of expansion (Lappe *et al.*, 1996). Neuron A responds maximally when the centre of expansion is located in the lower left hemifield. Vector-added unidirectional motion in this case is right-upward. The neuron also responds strongest when upward motion is presented transparently overlapping (right). Perceptually, and also at the population level in the model, this motion pattern results in an upward displacement of the centre of expansion, opposite to the location of the centre of expansion in the vector-summed stimuli. Yet, the response profile of the neuron is merely slightly rotated between the two conditions. The neuron in B shows an example of a larger rotation of the response profile. But it still does not perform a complete reversal.

projectors were used to define the boundaries of the receptive field for each neuron. For the data analysis, mean spike rate was determined for a 600-ms period beginning 400 ms after stimulus onset, and averaged over six to seven stimulus presentations.

Orientation and rotation of the response profiles was determined from the net vector response which was derived from the mean spike rates in the following way. Each response to one of the stimuli was regarded as a vector, the length of which was the amplitude of the neuronal response. The direction of the vector corresponded to the unidirectional motion that was used to construct the stimulus. For a transparent-overlap stimulus, it was the direction of the transparent unidirectional motion. For a vector-summed stimulus, it was the direction opposite to the location of the centre of expansion. The net vector was the vector sum of the eight individual response vectors. Its direction was the mean direction and its length the mean resultant length of the individual response vectors as derived using circular statistical methods (Batschelet, 1981). The direction of the net vector gave the direction along which the neuronal response changes maximally, i.e. the direction of the gradient of the neuronal response profile. Raleigh Z-statistics were used to determine the significance of the tuning (Batschelet, 1981).

Results

In perceptual judgements, the perceived locations of the centre of motion in the vector-summed and the transparent-overlap conditions

are in opposite directions (Duffy & Wurtz, 1993). In contrast, the majority of neurons in MST responded similarly to combined and transparent stimuli, when both contained uniform motion in the same direction. An example of this is shown in Fig. 2. This neuron responds best when the centre of motion in the vector-summed condition is in the lower left hemifield. In this case, vector-summed unidirectional motion is in the right-upward direction. But the neuron responds best to right-upward unidirectional motion in the transparent-overlap condition too, although the perceived location of the centre of motion is opposite in the two conditions.

At first glance, this result seems to contradict an involvement of area MST in optic flow perception. Like the example in Fig. 2, the behaviour of most neurons did not support the hypothesis that single cells shift or flip their response profiles. To investigate whether there might be a different explanation of how the responses of optic-flow-sensitive neurons in MST could contribute to the illusory transformation of optic flow fields, we derived predictions from model simulations.

The population-based model's response to the transparent-overlap stimuli has been found to parallel the results of human psychophysical experiments (Lappe & Rauschecker, 1995). Here we determined the responses of single neurons in this model to the transparent-overlap stimuli. We first presented the vector-summed stimuli (Fig. 1A, left) to the model neurons. We then presented the transparent-overlap stimuli (Fig. 1A, right) to the model neurons. The results of the simulations for two example model neurons are

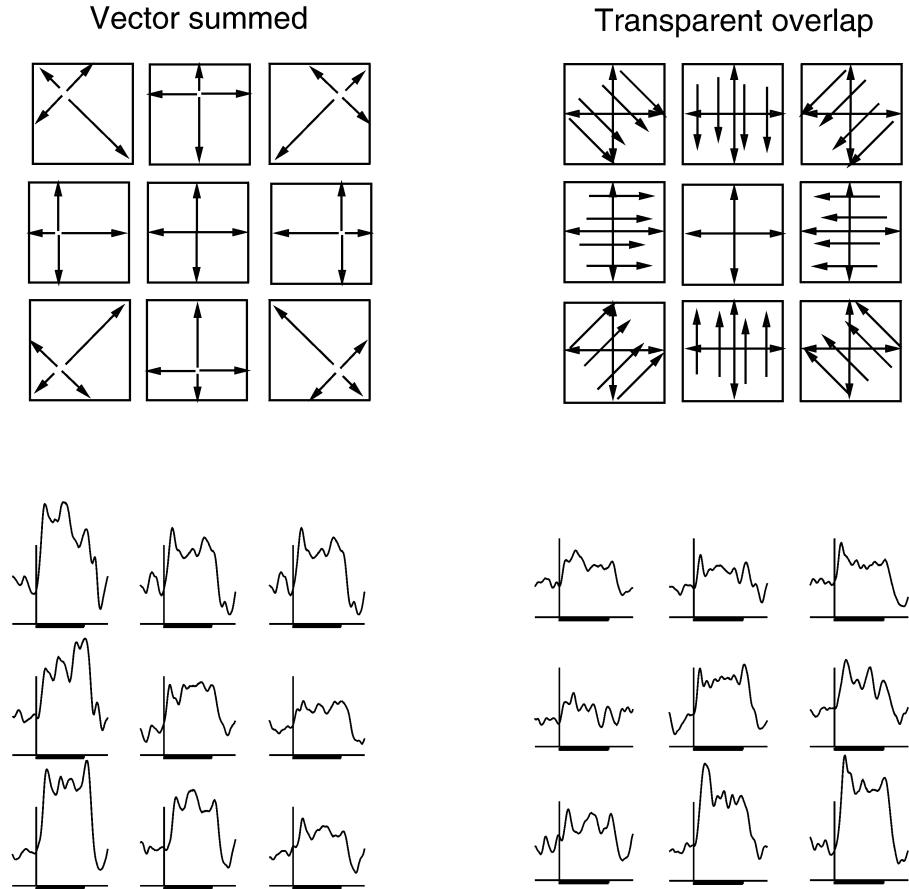


FIG. 4. Example of the rotation of the response profile in a single MST neuron. Conventions are the same as in Fig. 2. The neuron responded best to left centres of motion in the vector-summed stimuli. In the transparent-overlap condition the neuron responded best to upward and leftward motion. The best directions for vector-summed and transparently overlapping unidirectional motion are rotated against each other by $\approx 135^\circ$.

shown in Fig. 3A and B. The individual neurons show very different behaviour from the model population. Rather than shifting their response profiles in the direction of the overlapping unidirectional motion, the model neurons rotate their response gradients from the vector-summed response profile to the transparently overlapping response profile. The amount of rotation is different for the two neurons shown in Fig. 3A and B. For the neuron in Fig. 3A, the response profiles for vector-summed and transparent-overlap stimuli are very similar, with only a slight rotation between stimulus sets. The example in Fig. 3B shows a response profile rotation of $\approx 135^\circ$ between stimulus sets.

We tested whether the response profiles of single neurons recorded from area MST showed similar behaviour. Figure 2 already presented an example of a neuron that responded very similarly in the two conditions. This neuron exhibited little response profile rotation, maintaining high responses to the combination of centred centre of expansion and right-upward unidirectional motion (lower right graph in Fig. 2D left and right) with both stimulus sets, much like the model neuron in Fig. 3A. Figure 4 presents the responses of a different MST cell to the vector-summed and transparent-overlap stimuli. This neuron exhibited substantial response profile rotation similar to the model neuron in Fig. 3B. It gave strong responses to rightward vector-summed motion (left graphs in Fig. 4 left), and strong responses to left-upward transparent-overlap motion (lower right graph Fig. 4 right). Such strong rotations were encountered in a minority of neurons.

We determined the distribution of rotation angles of the response profiles in the model to derive a prediction for the response variation in the population. We performed 300 simulations of single model

neurons and calculated angles of rotation of the response gradients. Figure 5A shows a histogram of the distribution of rotation angles from model simulations. It is evident, that most often model neurons rotate their response profiles by only very small amounts or not at all. These findings were compared with the distribution of rotation angles of the response profiles of 228 MST neurons. Figure 5B shows a histogram of the distribution of rotation angles for MST neurons. Like the model neurons, the MST neurons mostly rotate their response profiles by small amounts. Thus, in both the model neurons and MST neurons, the rotation of the response profile is truly a graded effect across the neuronal population with a smooth and unimodal distribution.

In the model, such a rotation of the response profiles of single neurons is sufficient to result in the observed shift of the centre of expansion at the population level. The population activity is derived from the overlap of the response profiles of individual neurons. The shift of the population response is therefore the result of the combination of many individual response profiles. Figure 6 illustrates how a rotation of individual response gradients could result in a shift of the overlapping population activity. Neurons in the model are grouped in populations that encode different directions of heading, i.e. different locations of the focus of expansion. Each population has a preferred location of the focus of expansion. For the vector-summed stimuli, which contain a true centre of expansion, the response profiles of all neurons in one such population are arranged such that the neuronal responses cohere maximally when the centre of expansion is at the preferred location. The summed population activity then signals the centre of expansion at that position. In the transparent-overlap condition, the individual response profiles are rotated. To activate the same neurons coherently hence requires a

different stimulus: the response profiles in the model rotate such that coherent activation of the population is achieved when overlapping transparent motion is towards the preferred centre of expansion. Figure 7 shows this for a complete population of 32 neurons. This population encodes leftward heading directions. Accordingly, the

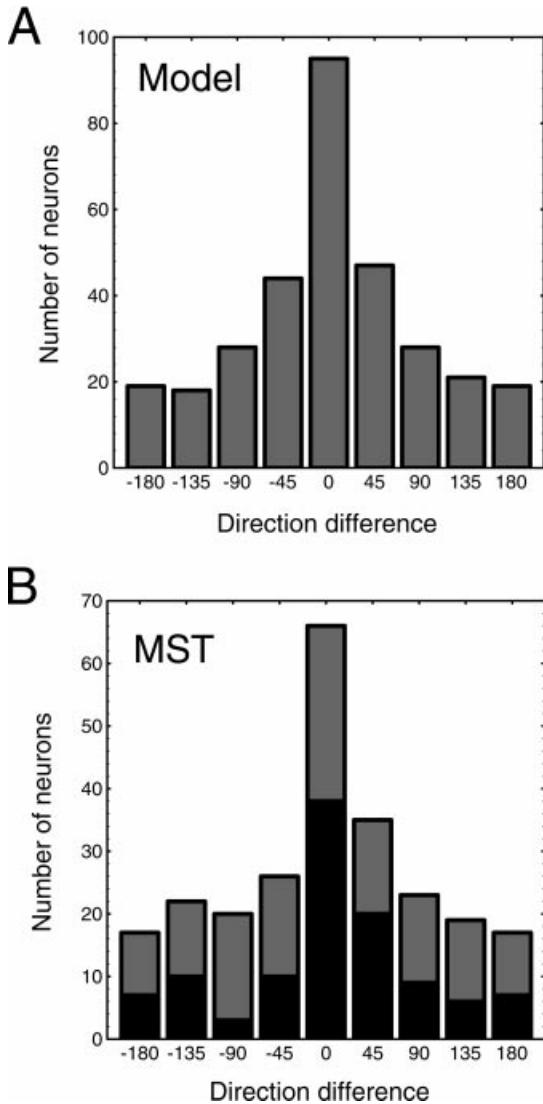


FIG. 5. Distribution of response profile rotation angles for 300 simulations of single model neurons (A) and 228 neurons recorded from area MST (B). For each model neuron simulation, the angle between the direction of the response gradient in the vector-summed condition and that in the transparent-overlap condition was determined to derive a prediction for the distribution of rotation angles in the population. The distribution peaks at zero, indicating that in most cases model neurons respond alike in the two conditions. To compare this with the MST recordings, the response of each recorded neuron to any of the eight vector-summed and the eight transparent-overlap stimuli was expressed as a vector. The direction of the individual response vector was the direction of the vector-summed or transparently overlapping unidirectional motion. The length was the firing rate of the neuron. Then, for each set of stimuli, the net vector of the responses was determined. The net vector indicates the direction that leads to the best response. It therefore corresponds to the direction of the response gradient in the model neurons. For each neuron, the angle between the net vector in the vector-summed condition and the net vector in the transparent-overlap condition was determined. The histogram shows the distribution of these angles. It matches the predictions obtained from model simulations. The results when all recorded neurons were included in the analysis are shown in grey. The black bars show the results when only those 103 neurons that showed a significant ($P < 0.05$) directional tuning for both stimulus sets independently were included in the analysis.

population response profile is most sensitive to leftward placements of the centre of expansion in the vector-summed stimuli (Fig. 7B, left). For the transparent-overlap stimuli, the rotation of the individual response profiles of the constituent neurons (Fig. 7A) results in a population response profile that is most sensitive to leftward overlapping motion (Fig. 7B, right).

In this way, the model suggests an explanation of how area MST could contribute to the perception of the transparent-overlap stimuli even though most MST neurons respond very similarly to the vector-summed and the transparent-overlap stimuli. If each neuron only contributes to the optic flow processing in the sense of a distributed population coding, small but systematic changes in the individual responses, like a small rotation of the response profile, could act together to induce the illusory percept. The model therefore suggests that it is the distribution of rotation angles, not the individual rotation of individual neurons, that subserves the perceptual effect.

Discussion

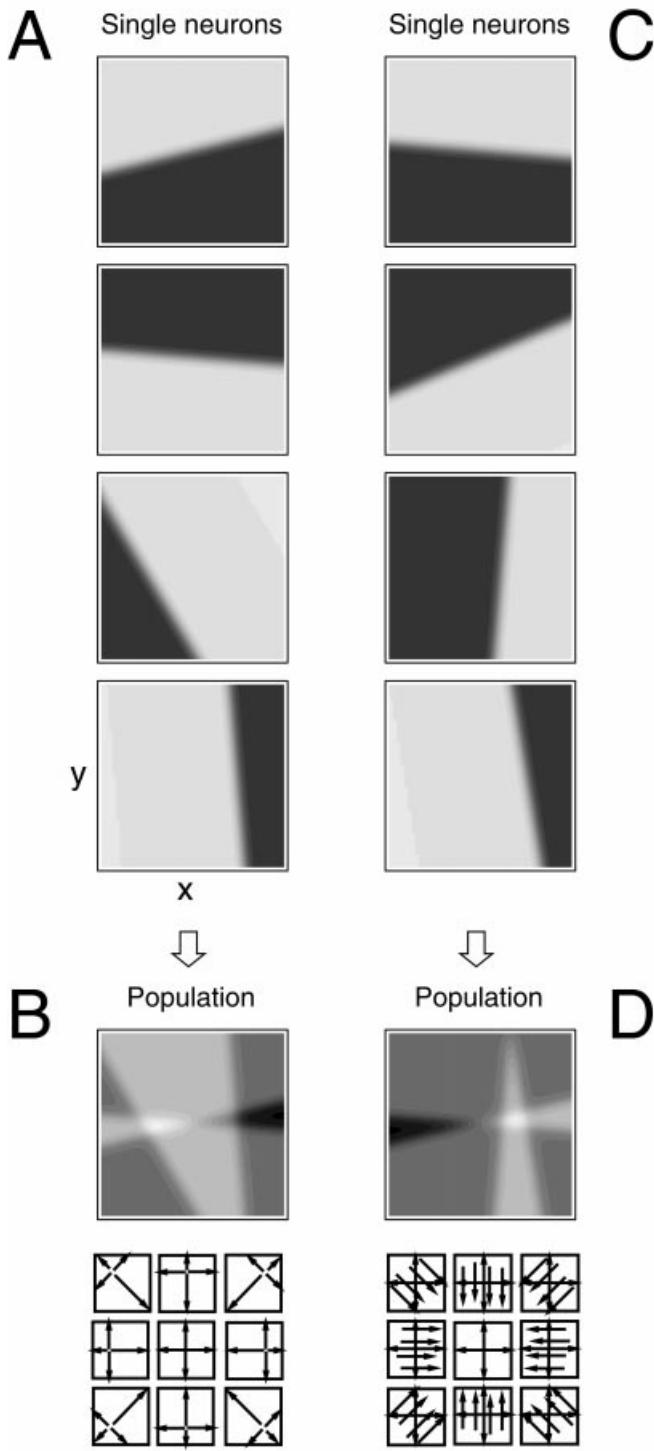
The work we have presented is concerned with the neural mechanisms of optic flow analysis. In area MST of the macaque monkey, many neurons are specialized in the processing of optic flow fields (Tanaka & Saito, 1989; Duffy & Wurtz, 1991). Their specific response properties have led to the suggestion that area MST is involved in the analysis of self-motion from optic flow (Duffy & Wurtz, 1995; Bradley, Maxwell, Andersen, Banks, & Shenoy, 1996; Lappe *et al.*, 1996). To understand how neuronal mechanisms can generate such complex response properties and can actually compute self-motion parameters, modelling studies have been helpful. Models can capture MST properties and link them to psychophysical investigation of heading perception (Lappe & Rauschecker, 1993; Perrone & Stone, 1994; Lappe *et al.*, 1996; Beintema & van den Berg, 1998; Zemel & Sejnowski, 1998). Here, we have used an illusory transformation of optic flow fields as a tool to gain insight into the neuronal processing. In this illusion, the location of the centre of a radial flow pattern is perceived to shift when transparent background motion is added (Duffy & Wurtz, 1993). This shift is also found in a model of optic flow processing for heading detection (Lappe & Rauschecker, 1995). We have used computer simulations of single model neurons to derive predictions that can be compared with neuronal recordings from area MST.

Area MST is believed to have an important role in the cortical analysis of optic flow. But for the illusory stimuli, the behaviour of single MST neurons is qualitatively different from the perceptual findings. The perceived centre of motion in the vector-summed and transparent-overlap conditions shifts, whereas the response profiles of single neurons in the two conditions are rotated against each other. The model reconciles this apparent mismatch. It reproduces both the single neuron behaviour and the perceptual shift. This shows that the graded response profile rotations observed in area MST can provide enough modulation to the distribution of neural activity to induce the illusory shift.

A remaining question is whether other models could similarly account for both the perceptual and physiological observations. Because the perceptual shift is consistent with visual heading estimation, many models of heading detection would be expected to show the perceptual effect. However, this is not necessarily the case for the behaviour of single neurons. Clearly, models in which individual neurons directly carry a preference for a certain direction of heading, e.g. by 'template-matching' (Perrone & Stone, 1994), would have a disadvantage, because they would predict that individual neurons should shift or flip between the two stimulus

sets. However, it might be possible to embed this behaviour in a population coding scheme and remedy the mismatch. Zemel & Sejnowski (1998) have presented a model that can simultaneously compute different object motions and self-motion. They suggest that this model could account for the perceptual shift if a suitable neuronal module is added, but the properties of the neurons in such a module are not known at present.

Our results have implications for the understanding of the analysis of optic flow by area MST. We have previously proposed that the illusory transformation of optic flow fields results from an attempt of



the visual system to compensate for eye movements that might disturb optic flow fields generated during self-motion (Duffy & Wurtz, 1993; Lappe & Rauschecker, 1995; Grigo & Lappe, 1998). Pursuit eye movements add unidirectional motion to the retinal image of optic flow, creating a disassociation of the centre of motion and the direction of heading (Koenderink & van Doorn, 1976; Longuet-Higgins & Prazdny, 1980; Regan & Beverly, 1982; Warren & Hannon, 1990). To see how this might be related to the perceived shift of the centre of motion in the transparent-overlap stimulus, it is useful to consider whether this stimulus might be generated by a particular self-movement in a specific visual environment. Indeed, computer simulations have shown that the transparent stimulus can be regarded as the result of a self-movement into the direction of the illusory centre of expansion in combination with an eye rotation (Lappe & Rauschecker, 1995). Consider an observer moving towards a frontoparallel plane of random dots. If his heading is towards the left, a radial motion pattern is generated in which the focus of expansion appears in the left visual field. When the observer rotates his eyes rightward during the movement, the eye rotation will induce leftward visual motion which is vector-summed with the radial pattern. The centre of expansion is then shifted towards the centre of the visual field, although the direction of heading remains on the left. Direction of heading and centre of expansion become disjointed. Now consider a second plane of random dots located very far distant from the observer. The translational movement of the observer causes only a negligible radial motion of these dots because of their distance from the observer. The eye rotation, however, induces a uniform leftward motion of the entire second set of dots. The combination of both dot movement patterns approximates the transparent-overlap stimulus. The centre of expansion in this case is perceived to lie in the direction of the overlapping motion, i.e. on the left. This is consistent with the direction of heading which also lies on the left. Therefore, when one considers the stimulus as a result of self-motion, the perception of the human subjects is veridical in the sense that they perceive the centre of the radial motion to be located in the direction of heading, much as a regular focus of expansion (Gibson, 1950). Subsequent psychophysical experiments that tested predictions from this hypothesis have provided more evidence. When the stimulus is presented stereoscopically, such that the two groups of dots appear to lie at different depths by means of relative disparity, the strength of the illusion depends on the foreground/background relationship. When the

Fig. 6. Schematic illustration of how single neuron responses in the model contribute to the population encoding of the perceived centre of expansion. We consider four individual neurons that are part of a population of neurons that encodes a leftward heading direction. (A) Response profiles of individual neurons for the vector-summed stimuli. They are shown as greyscale maps which view 3D surface plots, as in Fig. 3, from above. Brightness represents response activity, x and y are horizontal and vertical speed of the unidirectional motion, or horizontal and vertical position of the centre of expansion, respectively. (B) Population response profile obtained from summing the responses of the four neurons. The individual response profiles in A are differently orientated such that they maximally overlap at a position left of the centre. The population reaches peak activity when the centre of motion is at that point, i.e. the heading is to the left. (C) Response profiles of the same four neurons for a presentation of the transparent-overlap stimuli. The directions of the individual response gradients are slightly rotated by different amounts. Note that none of the response profiles actually flips. (D) The summation results in a different population response profile. Maximum activity, i.e. optimum overlap of the rotated profiles, is reached when transparently overlapping unidirectional motion is to the left. Thus, the population that responds best to leftward heading in the vector-summed stimuli also responds best to overlapping leftward motion in the transparent-overlap condition, i.e. to a stimulus that induces the percept of a leftward shift of the centre of motion.

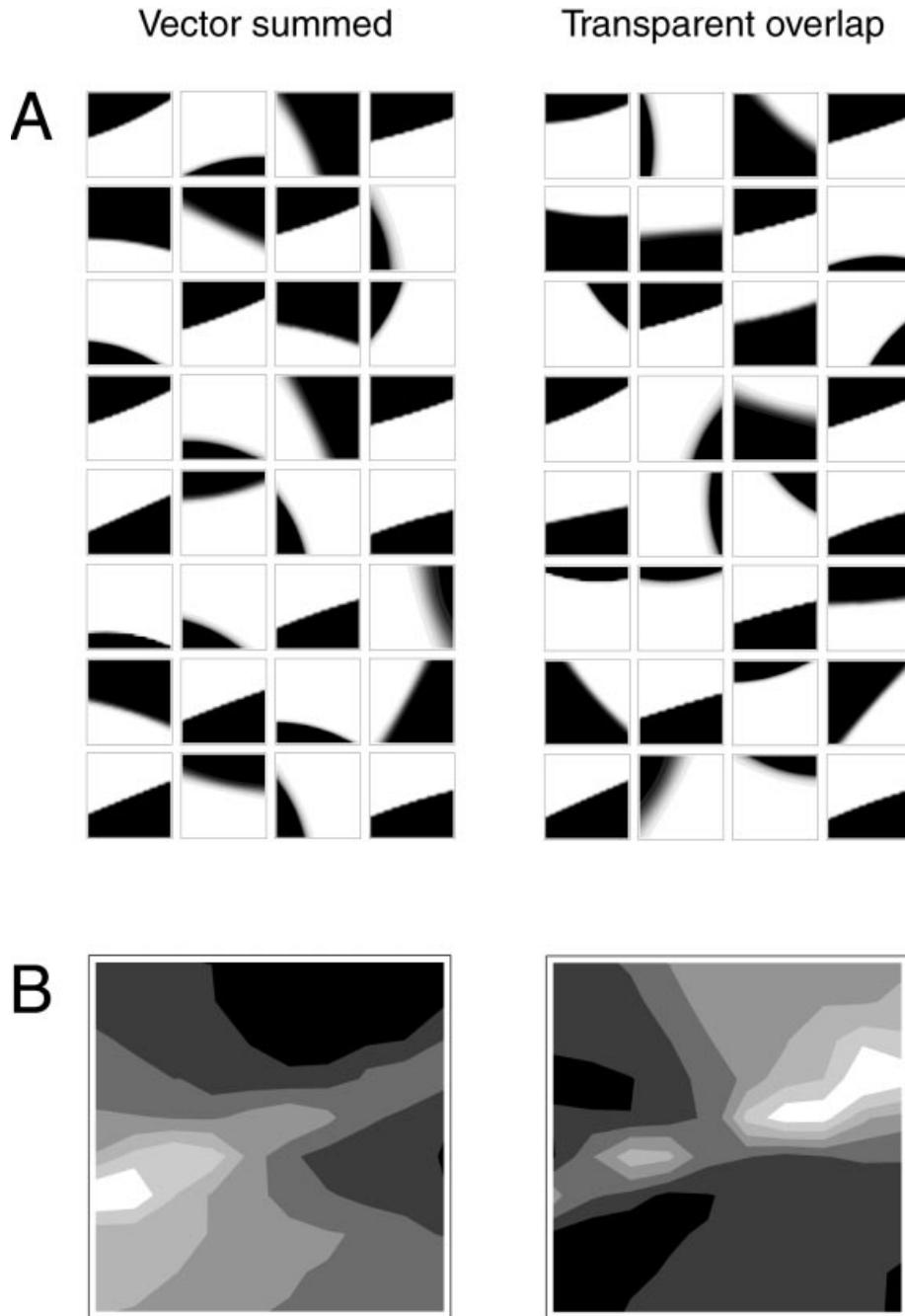


FIG. 7. Individual and aggregated response profiles for an entire population of model neurons. (A) The population consists of a total of 32 neurons. The plots show their individual response profiles to the vector-summed and the transparent-overlap stimuli. (B) Population response profiles obtained from summing the responses of all neurons for the two stimulus conditions. For the vector-summed stimuli, the population reaches peak activity when the centre of motion is on the left. For the transparent-overlap stimuli, the individual neuronal response profiles rotate such that the population response profile is approximately inverted. Peak activity is reached on the right side of the plot, i.e. when overlapping transparent motion is to the left, consistent with the populations preferred response to a centre of motion that is perceived on the left.

transparent-overlapping motion is in front of the radial motion, i.e. when stereoscopic vision signals a conflict with the described self-motion scenario, the magnitude of the shift is reduced by 75% (Grigo & Lappe, 1998).

In the above interpretation of the illusory shift, the transparent unidirectional motion would be regarded as a re-afferent eye movement signal. The model exploits this visual information for recreating the effects of the illusory transformation. The fact that single model neurons and the recorded data from area MST are very similar suggests that neurons in area MST might also be able to use visual information for heading detection in the presence of eye movements. Optic-flow-sensitive neurons in area MST can compensate for the modifications of the optic flow that are introduced by smooth-pursuit eye movements (Bradley *et al.*, 1996). In the presence of real-pursuit eye movements the eye movement signal used for the

compensation is derived from extraretinal information. In the case of our transparent stimuli, such a signal would have to be derived from the visual input, not from extraretinal sources. The transparent unidirectional motion provides such a visual eye movement signal. This could suggest that area MST might also use visual cues for the computation of self-motion from optic flow.

The perceptual shift of the centre of expansion in the model relies on a population read-out of single neuron activities. Individual model neurons respond to the transparent-overlap stimuli but their response characteristics do not directly reveal the perceptual shift. The responses of the individual neurons lead to the shift only when combined in the population activity. This implies that the perceptual shift is an emerging property of the population heading map proposed in the model. The population activity represents a further synthesis of neuronal activity that can exhibit original behaviour such as the here-

described optic flow illusion. Our results suggest that the function of a cortical area may not only be determined by the properties of the single neurons within it, but also by the code by which the neuronal responses are read out.

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Abbreviations

MST, medial superior temporal (area of monkey extrastriate visual cortex); MT, middle temporal (area).

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