

## Integration of motion cues for the initiation of smooth pursuit eye movements

Richard T. Born\*, Christopher C. Pack and Ruilin Zhao

*Department of Neurobiology, Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115-5701, USA*

**Abstract:** To clearly see a moving object, an observer must rotate his or her eyes with a velocity that matches that of the object. Such rotations are called smooth pursuit eye movements, and they depend critically on the ability of the primate brain to integrate information about object velocity from various local motion signals. When the local motion signals are in conflict, it is possible to use smooth pursuit eye movements as a continuous read-out of the motion integration process. This review discusses the results of recent behavioral experiments that have taken this approach, along with relevant neurophysiological and computational studies.

**Keywords:** Motion integration; Aperture problem; Eye movements; Smooth pursuit; Ocular following

### Introduction

Smooth pursuit is an important oculomotor behavior that allows a moving object to be held relatively stationary on the fovea so that it may be analyzed with high spatial acuity; see Eckmiller and Bauswein (1986), Lisberger et al. (1987), Keller and Heinen (1991) and Ilg (1997) for general reviews of smooth pursuit eye movements. The neural system that accomplishes this feat has been widely studied by both physiologists and psychologists because of the ease and precision with which its outputs (i.e. eye movements) can be measured, the ready manipulability of the inputs (i.e. visual stimuli), and, most significantly for this review, because of its intimate connection with visual motion processing. Because of this last fact, the behavior can serve as a convenient read-out of the algorithms at work on the

sensory side. However, because the steady-state behavior of any closed-loop system, such as pursuit, is dominated by the very presence of negative feedback (Carpenter, 1988), it has mainly been the *initiation* of pursuit (or other ‘open-loop’ conditions) that has served this purpose.

The visual stimulus that drives the initiation of pursuit is target *motion* on the retina, or retinal slip (Rashbass, 1961). Such motion generates a number of visual ‘error signals’, including position, velocity and acceleration errors, all of which are involved in both the initiation and maintenance of the behavior, though retinal velocity error is the most important (Lisberger and Westbrook, 1985; Morris and Lisberger, 1987). Traditionally, these basic properties of pursuit have been studied in the laboratory by measuring the movements of the eyes in response to a single moving target, usually a small spot, presented against a dark, featureless background.

In the real world, however, the situation is more complicated. Often there are multiple possible targets present simultaneously, any given target may have an irregular shape — thus generating ambiguous and conflicting local motion signals — and

---

\* Correspondence to: R.T. Born, Department of Neurobiology, Harvard Medical School, 220 Longwood Avenue, Boston, MA 02115-5701, USA. Tel.: +1-617-432-1307; Fax: +1-617-734-7557; E-mail: rborn@hms.harvard.edu

target and eye motion usually occur against a richly textured background. All of these features present interesting problems that must be solved at the sensory end before useful motor signals can be generated. How does the brain combine numerous local motion measurements to produce a veridical global direction of object motion that can be tracked by the eyes? Our review will focus on this question and what studies of pursuit eye movements have contributed to its answer.

Most of the results to be discussed below have been obtained in both monkeys (usually rhesus macaques) and humans. The chief advantage of the human preparation is that it allows one to compare, directly and relatively easily, the relationship between the *perception* of visual motion and a visually guided *behavior* that depends upon an internal representation of visual motion (Kowler and McKee, 1987; Watamaniuk and Heinen, 1999). While this has been an interesting and fruitful approach, for present purposes we will leave aside the question of whether these two brain ‘functions’ — perception and movement — make use of exactly the same representations or not. Suffice it to say that there appears to be a broad degree of overlap (Watamaniuk and Heinen, 1999; Beutter and Stone, 2000) but that the particular exigencies of each function would naturally lead to some differences depending on precisely how they are measured and compared; e.g. Mack et al. (1979).

Experiments in non-human primates, on the other hand, have the advantage of permitting comparisons between neuronal signals in motion processing regions of monkey visual cortex (most prominently, the middle temporal, MT, and the middle superior temporal, MST, visual areas, but in other parietal and frontal areas as well; see Keller and Heinen, 1991 for an overview) and the eye movements evoked by the same or similar stimuli. Virtually all studies of this nature have pointed to a very tight link between the neuronal properties in these two areas and the initiation of both smooth pursuit (Newsome et al., 1985; Dursteler and Wurtz, 1988; Komatsu and Wurtz, 1988, 1989; Movshon et al., 1990; Bremmer et al., 1997; Ferrera and Lisberger, 1997b; Groh et al., 1997; Lisberger and Movshon, 1999; Recanzone and Wurtz, 1999, 2000; Born et al., 2000; Pack and Born, 2001) and ocular following (Kawano et al.,

1994; Kawano, 1999). Because of this relationship, we will also include a brief discussion of the relevant neuronal data.

### Combining motion vectors: multiple targets

As noted above, in the majority of pursuit experiments, only a single, simple target is present in the field of view at any given time. One way to examine motion integration is to introduce a second simple target and to ask how the system treats the two associated motion vectors. This approach has been taken by two different labs (Ferrera and Lisberger, 1995, 1997a; Lisberger and Ferrera, 1997; Recanzone and Wurtz, 1999, 2000) with largely consistent results. If the two targets are presented nearby in both space and time and the animal has no prior knowledge to indicate which of the two targets is to be pursued, the read-out is a simple *vector average* of the two motion vectors (Ferrera and Lisberger, 1997a). If, however, the animal is supplied with prior knowledge concerning which target is to be pursued, it can use attention to suppress the motion vector from the irrelevant target (the ‘distracter’) thus producing a *winner-take-all* pursuit response (Ferrera and Lisberger, 1995).

Even with prior knowledge that ultimately allows for target selection, it appears that the earliest pursuit response is one of vector-averaging and that effects of attention appear only after some time (Recanzone and Wurtz, 1999). This was discovered by studying pursuit initiation (and the responses of neurons in MT and MST) during a task that required a monkey to track one of two possible visual stimuli: a ‘target’ and a ‘distracter’. The animal had to identify which stimulus was the appropriate target (based on its shape) and then follow it. When both the target and the distracter moved simultaneously within the same region of retinal space (which was within the receptive field of the neuron under study), the authors were able to examine how these two visual motion signals were combined, both by the pursuit system, as indicated by the eye movements made by the monkey, and by the neurons. Interestingly, both measurements revealed that a vector average was used to combine the two signals when the two stimuli appeared within the receptive field for only a short time (a ‘gap’ of 150 ms) before the animal

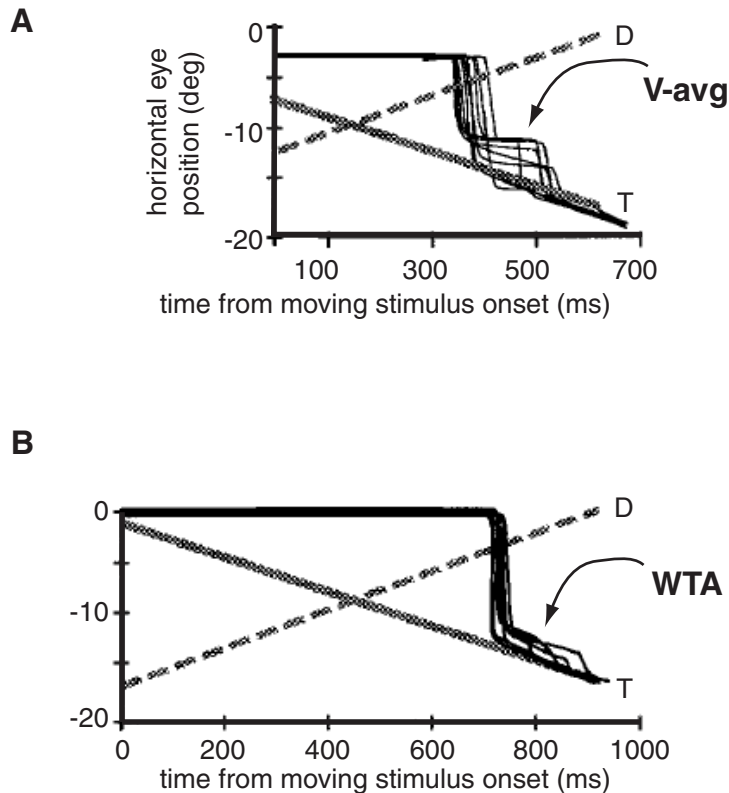


Fig. 1. Combining velocity vectors from two objects. (A) When a pursuit target (T) and a distracter (D) appear near each other in space and time, the resulting pursuit eye movement is a vector average (V-avg) of the two velocity vectors. (B) When the two objects appear well in advance of the cue to track and are separated by a greater distance, the distracter is effectively ignored and the pursuit shows a 'winter-take-all' (WTA) integration strategy, with the target winning. Modified from fig. 2 of Recanzone and Wurtz (1999).

was instructed to make the eye movement (Fig. 1A). If the two stimuli appeared further apart and for a longer time (450 ms) before the animal was cued to make the eye movement, both the neurons and the pursuit 'behaved' as if the appropriate target was the only stimulus present (i.e. a winner-take-all method of combining the motion signals from the target and the distracter, with the target winning; Fig. 1B). It was as if, quite sensibly, the extra time had allowed the system to distinguish target from distracter and then suppress the response to the distracter's motion.

Very similar results were obtained when the two motion vectors were produced by a single visual target and a second 'virtual' target introduced by microstimulating direction columns in MT (Groh et

al., 1997; Born et al., 2000; Fig. 2). In these experiments, the animal was required to pursue a single moving target that appeared within the receptive field of a given column of MT neurons. On half of the trials, the neurons at the site were activated for approximately 200 ms beginning at the onset of target motion. The interactions between the microstimulation and multiple different target velocities were studied at each site. Under these conditions, most comparable to those used by Lisberger and Ferrera in their 1997 paper and to the short-gap condition of Recanzone and Wurtz (1999), the pursuit response again proved to be a weighted average of the target velocity vector and an 'electrical' velocity vector introduced by the microstimulation. This computa-

?#1

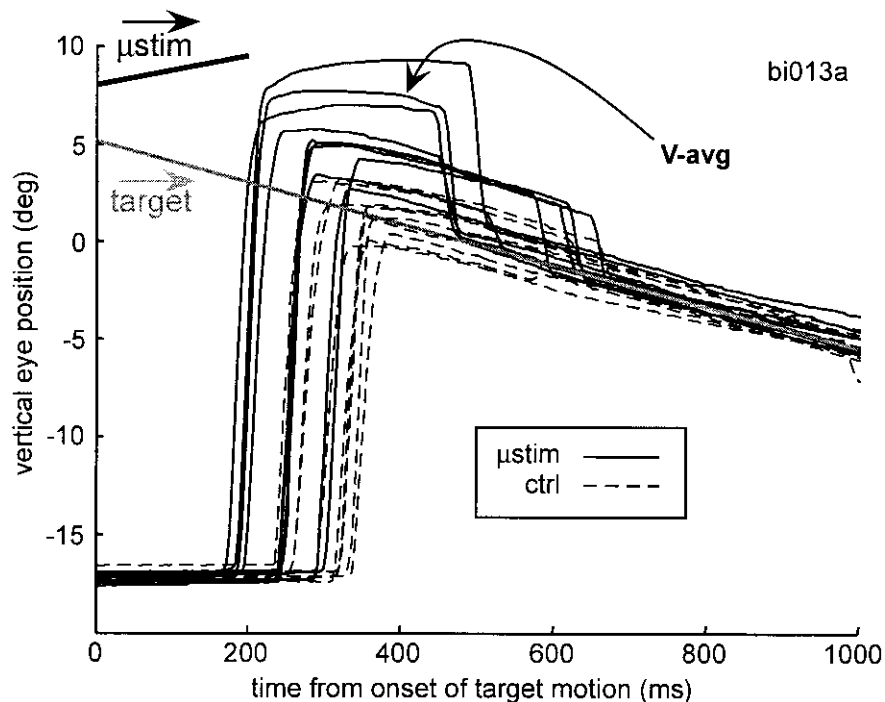


Fig. 2. Combining velocity vectors due to target motion and microstimulation of MT. On all trials the animal was required to track a small spot moving downwards at  $10^\circ/\text{s}$ . The resulting pursuit eye movement is a vector average (V-avg) of the two velocity vectors. In this case the 'electrical' vector introduced by microstimulation (biphasic current pulses of  $40 \mu\text{A}$  at  $200 \text{ Hz}$  for  $\sim 200 \text{ ms}$ ) was upwards at approximately  $8^\circ/\text{s}$ . This vector was determined by a multivariate regression analysis of the interaction of microstimulation with 9 different target velocities ( $p < 0.00001$ ), all of which were randomly interleaved with the trials shown.

tion appears to be quite widespread and robust, as the vector-averaging model best describes a large number of microstimulation experiments at different sites in MT (Groh et al., 1997; Born et al., 2000) and using a wide range of current amplitudes and pulse frequencies (R. Zhao and R.T. Born, unpubl. observations).

Additional support for vector-averaging comes from measurements of human pursuit initiation in response to random-dot cinematograms, i.e. large fields ( $10^\circ$ ) containing many (250) moving dots, each of whose direction was randomly chosen from a distribution of possible directions (Heinen and Watamaniuk, 1998; Watamaniuk and Heinen, 1999). For this type of stimulus no single dot provides consistent or veridical motion information, yet human observers are able to integrate over space and time and perceive smooth motion in the direction that corresponds to the *average* of the distribution (Williams and Sekuler, 1984). When humans are asked to track the motion

in such displays with their eyes, they similarly pursue the statistical mean with great accuracy, exceeding that to a single target moving at the same velocity (Heinen and Watamaniuk, 1998; Watamaniuk and Heinen, 1999).

#### Combining motion vectors: complex shapes

Another approach to the problem of motion integration for pursuit eye movements is to use visual stimuli whose shape generates local motion vectors that differ from the velocity of the object ('global' motion). The reason that this generates an interesting problem for the pursuit system is that all of the available visual information is from neurons, such as retinal ganglion cells, with very small and discrete receptive fields. Thus the object's contours are effectively seen through many tiny apertures which make explicit only the component of motion perpendicular to the contour (Fig. 3). This 'aperture problem'

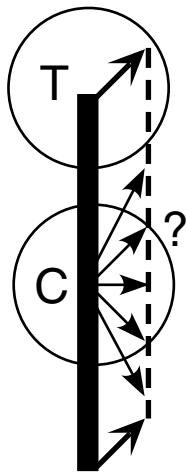


Fig. 3. Receptive field 'apertures' create ambiguous local motion signals. For a vertical bar moving upwards and to the right, a neuron with a small receptive field positioned along the contour (C) can measure only the rightward component of motion. This measurement is ambiguous, because it is consistent with many possible directions of actual bar motion. Only neurons whose receptive fields are positioned over the bar's terminators (T) can measure the direction of motion accurately.

must be solved by taking into account the motion of object features, called terminators, whose local motion is unambiguous. Furthermore, this information must be integrated in a way that ultimately allows terminator-based motion signals to prevail.

Inspired by the work of Lorençeau and colleagues (Lorençeau et al., 1993), who originally used such stimuli to study motion perception, a number of labs have recently used complex shapes to elicit both short-latency ocular following in humans (Masson et al., 2000) and smooth pursuit eye movements in monkeys (Pack and Born, 2001) and humans (Masson and Stone, 2002). The basic findings were similar in all cases: the initial direction of the pursuit (or ocular following) was strongly biased by the orientation of the contour, and the resulting eye movement looked like a weighted average of both terminator- and contour-based signals. Over time, the behavior evolved to follow the true direction of object motion, a situation that can be thought of as a winner-take-all computation, with the terminator motion winning.

A specific example of this 'contour effect' is shown in Fig. 4. In this case a macaque monkey, after a brief fixation period, was required to track the

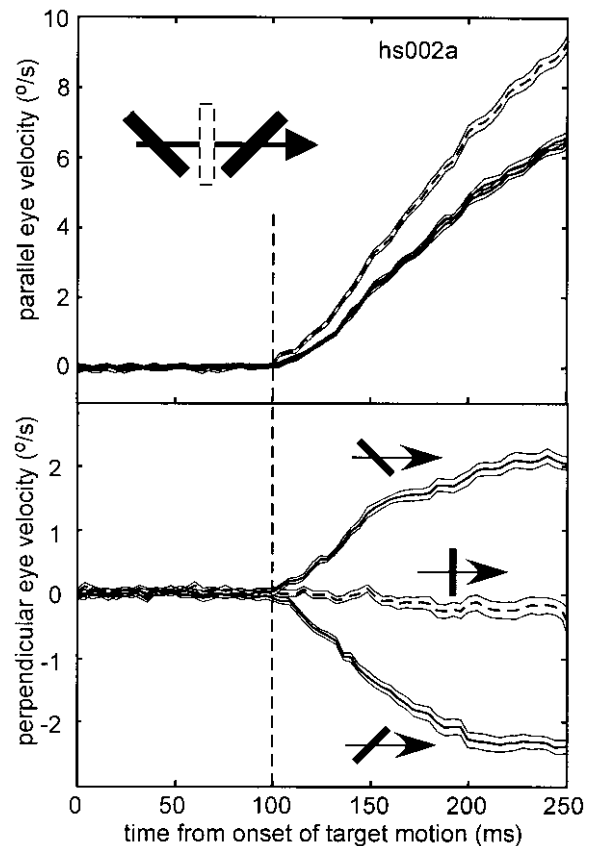


Fig. 4. Effect of contour orientation on the initiation of smooth pursuit. The animal was required to track the center of a long ( $25^\circ$ ) bar moving in one of four possible directions at  $10^\circ/\text{s}$ . When the bar's orientation was perpendicular to its direction of motion (green traces), pursuit was purely in the direction of bar motion with no perpendicular component. When the bar was tilted (red and blue traces), the initial pursuit eye movement deviated in a direction perpendicular to the orientation of the contour. Each thick line represents the mean; thin lines represent  $\pm 1$  standard error of the mean.

center of a moving bar that appeared at the fovea and could then move off in one of four different directions at a speed of  $10^\circ/\text{s}$ . The moving bar could assume one of three different orientations with respect to its direction of motion: perpendicular or tilted either backwards or forwards by  $45^\circ$ . For each different direction of target motion the eye movement data are represented as the component *parallel* to the direction of bar motion (Fig. 4, upper panel) and the component *perpendicular* to the direction of bar motion (Fig. 4, lower panel), thus allowing

data from different directions of bar motion to be combined. (There was no systematic effect of target direction on the contour effect.) For simplicity, one can think of the data *as if* the direction of motion on all trials were purely rightward, so that any vertical eye movements represent a deviation from the true direction of target motion. Thus when the bar's orientation was vertical (control, green traces), the pursuit was only to the right with no vertical component as would be expected for any other simple moving target. If, however, the horizontally moving bar was tilted (blue and red traces), the initial pursuit deviated in a direction perpendicular to the contour orientation. This deviation is present in the very earliest phase of pursuit initiation (dotted line), and it persists for approximately 150 ms, depending on a number of factors such as bar length (see below), speed and contrast. One additional point worth noting is that the initial *horizontal* pursuit is slower for the tilted bars than for the vertical bars and by exactly the amount predicted by the stimulus geometry and the aperture problem; i.e. the two curves superimpose if the vertical bar-pursuit values are multiplied by cosine ( $45^\circ$ ). This fact was not illustrated in our original publication (see fig. 3b of Pack and Born, 2001) due to the use of a small subset of eye movement trials from a single monkey.

If the initial response is simply a weighted average of contour- and terminator-related motion signals, then stimulus manipulations that change the relative amounts of the two signal types should produce predictable changes in the behavior. This has proven to be the case. For example, Masson et al. (2000) reduced the relative strength of the terminator signals by blurring the line endings and found a corresponding decrease in the amplitude of the terminator-driven component of ocular following. Conversely, Pack and Born, 2001 (Fig. 5) found that increasing the relative proportion of contour signals, by using longer bars, created a progressively larger contour-orientation bias in pursuit initiation. This latter experiment revealed that the pursuit system is capable of rapidly integrating along contours over very large regions of the visual field, extending to at least 35 degrees. This last result is also consistent with the aforementioned studies of human pursuit of random-dot cinematograms (Heinen and Watamaniuk, 1998), in which increasing the size of the dot

field led to increases in the initial eye acceleration and decreases in pursuit latency.

In keeping with the close relationship between open-loop pursuit and signaling within visual motion cortex, Pack and Born (2001) found a neural correlate of this behavior in MT of the alert monkey. The earliest directional responses, beginning about 80 ms after the onset of stimulus motion, primarily encoded the component of motion *perpendicular* to the orientation of the contour (Fig. 6A). That is, they were strongly affected by the ambiguous contour signals. However, the later responses ( $>140$  ms after motion onset) encoded the true direction of motion, regardless of contour orientation (Fig. 6B). Thus the responses of MT neurons reflect a similar solution of the aperture problem for motion over a period of about 60 ms. While this time-course is considerably faster than that found for pursuit, the bar-fields used to characterize the neurons contained many individual bars that were considerably shorter ( $3^\circ$ ) than the single bar used in the pursuit experiments, thus presenting a considerably greater proportion of terminator signal. Indeed, preliminary data from our lab indicate that increasing the length of the bars prolongs the neural solution in the same way that it affects pursuit behavior (Fig. 5).

Interestingly, the same MT neurons, when studied in animals lightly *anesthetized* with isoflurane, completely failed to solve the aperture problem, even though they remained vigorously responsive and sharply tuned for direction of motion (Pack et al., 2001; Fig. 6C). Some have argued, based on contextual effects measured in primate V1 (Lamme et al., 1998a,b), that neural processes evolving over tens of milliseconds and highly susceptible to general anesthetics indicate a role for *feedback* from higher cortical areas. In the case of the neural and pursuit effects described above, this would implicate higher motion-processing areas such as the medial superior temporal (MST) or lateral intraparietal (LIP) areas. Both of these areas contain at least some neurons that have large direction-selective receptive fields (Saito et al., 1986; Komatsu and Wurtz, 1988; Blatt et al., 1990) and both have feedback connections to MT (Felleman and Van Essen, 1991). If the feedback hypothesis is correct, it should be possible to selectively impair the integration process by inactivating one or both of the regions. A second possibility,

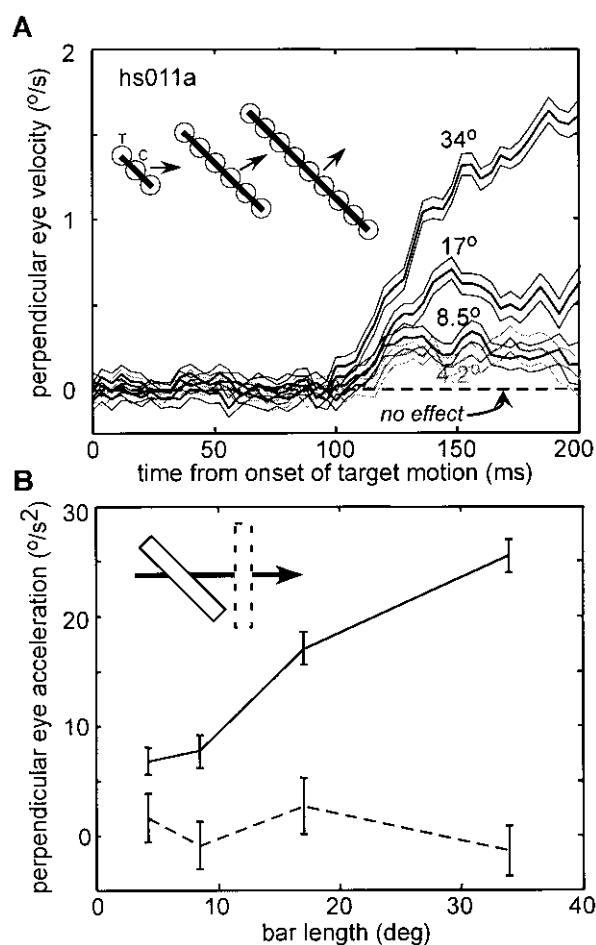


Fig. 5. Effect of bar length on the contour effect. (A) In this experiment, bars of different lengths and different relative orientations were randomly interleaved. For simplicity, only the component of the eye movement *perpendicular* to the direction of bar motion is plotted. Thus the control trials (bar moving perpendicularly with respect to its axis of orientation) show no velocity component in this direction (dotted line in A). The length of the bar has no effect on the latency of pursuit initiation, but has a clear effect on the initial slope (i.e. acceleration). Traces represent mean eye velocity  $\pm$  the standard error of the mean. (B) The initial (0–40 ms) deviation in the eye acceleration is plotted as a function of bar length for both tilted bars (solid line; the 45° and 135° tilt data have been pooled) and for bars moving perpendicular to their axis of orientation (dashed line). Acceleration was calculated as the slope of a regression line fit to the first 40 ms of pursuit for each single trial. Error bars represent the standard error of the mean of the single-trial slope values.

however, is that general anesthesia has a selective effect on a parallel stage of processing for terminator motion (Wilson et al., 1992). The second visual area, V2, is a good candidate for this so-called ‘indirect’ route to MT and the pursuit system with tantalizing, though inconclusive, findings regarding physiology (Levitt et al., 1994a; Mareschal and Baker, 1998), anatomy (Maunsell and Van Essen, 1983; DeYoe and Van Essen, 1985; Shipp and Zeki, 1989; Levitt et al., 1994b; Yabuta et al., 2001; see Born, 2001 for an

overview) and function (Merigan et al., 1993). This hypothesis, too, should be testable with the appropriate inactivation experiments. Having both a robust neural and a behavioral correlate of this phenomenon should facilitate studies of its mechanism.

#### Combining motion vectors: complex motion

Yet another way to analyze motion integration for pursuit is to study initiation in response to more

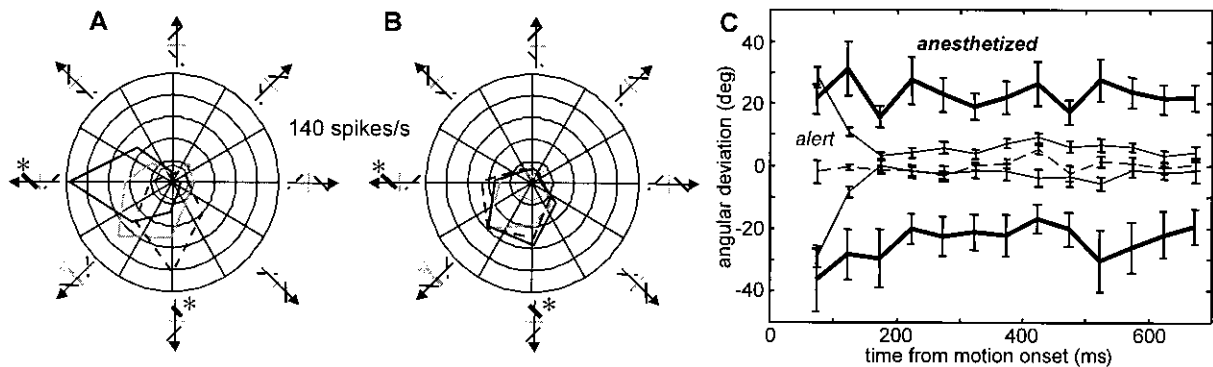


Fig. 6. MT and the aperture problem. (A) Over the first 20 ms of the directional response (65–85 ms after the onset of stimulus motion), the direction tuning reflects the component of motion perpendicular to the contour's orientation ( $\odot$ ), whereas later responses, >140 ms after onset of target motion (B) are similar regardless of the orientation of the moving bars. (C) The population of MT neurons in the alert monkey ( $n = 60$ ) converges to an orientation-invariant representation over about 60 ms; neurons recorded in the anesthetized animals never converge, even though their responses are equally vigorous and direction-selective. Modified from fig. 2 of Pack and Born (2001). Anesthesia data are from Pack et al. (2001).

complicated moving stimuli, such as those combining 1st and 2nd order motion cues (Lindner and Ilg, 2000; Hawken and Gegenfurtner, 2001). In these experiments, visual stimuli consisting of either 1st order motion (spatiotemporal changes in luminance) or 2nd order motion (spatiotemporal changes in, for example, texture or motion; see Chubb and Sperling, 1988; Cavanagh and Mather, 1989), or a combination of the two were used to create pursuit targets for human subjects. In both of these studies, pursuit initiation was better (i.e. higher gain) to 1st order than to 2nd order stimuli, though this difference was less marked at faster target speeds (Hawken and Gegenfurtner, 2001; Fig. 7). When the two types of motion were combined, 1st order motion dominated the earliest pursuit responses even though subjects were instructed to track the 'object' (i.e. 2nd order) motion, in some cases resulting in an initial eye movement in the wrong (1st order) direction (arrows in Fig. 7).

More recently, a similar approach has been used to study short-latency ocular following in humans (Masson and Castet, 2002). In this case the authors used 'uni-kinetic' plaids consisting of a drifting grating superimposed on a stationary grating tilted  $45^\circ$  with respect to the moving grating. This stimulus has the very useful property of producing conflicting motion signals: '1D' or contour motion signals in one direction (e.g. upwards in Fig. 8) and '2D' or pattern motion signals at a  $45^\circ$  angle (upwards and

rightwards in Fig. 8). With these stimuli Masson and Castet (2002) observed that the earliest responses were completely dominated by the 1D direction, but, after a delay of about 25 ms, the eye movement direction deviated to reflect the influence of the pattern direction signals. Not only did they observe a clear latency difference for the 1D- versus 2D-related ocular responses, but they also found that the contrast response functions (CRFs) for the two components were completely different. The 1D CRF was steep and saturated at low contrast, similar to the contrast sensitivity function for magnocellular neurons in the lateral geniculate body (Derrington and Lennie, 1984), while that for the 2D response was much shallower and non-saturating, similar to the corresponding function for parvocellular neurons. Taken together, these results constitute the best evidence to date for parallel motion channels driving smooth eye movements, and they mesh nicely with certain computational models of higher-order motion integration.

### Models and the neural substrate

Because pursuit initiation is an open-loop behavior, it is convenient to analyze it as a succession of processing stages. Conceptually, pursuit initiation can be subdivided into three computational stages. The first stage represents local motion vectors of the kind that might be generated by a moving object.



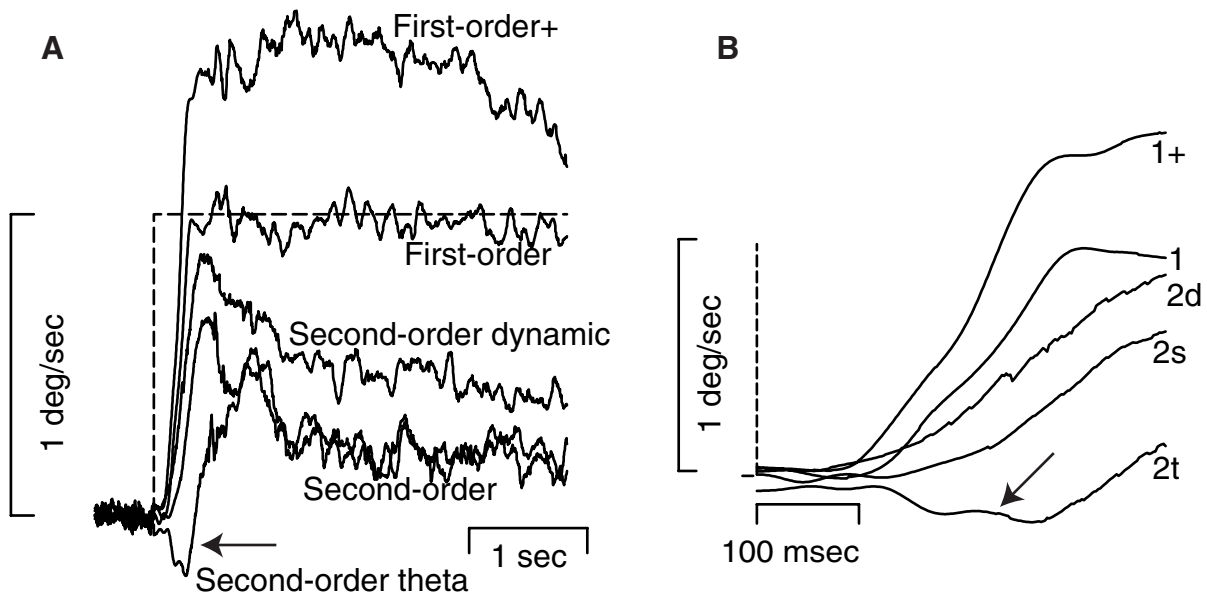


Fig. 7. Human pursuit initiation to targets defined by 1st or 2nd order motion stimuli. The gain of the initial phase of pursuit (B) is greatest for 1st order motion (1) and diminished for different varieties of 2nd order motion (2d, 2nd order dynamic; 2s, 2nd order static; 2t, 2nd order theta). Dashed lines show the target velocity profile. Note that for 2nd order theta motion, for which 1st and 2nd order motion directions are opposed, the initial eye movement is in the 'wrong' (1st order) direction (arrows). Adapted from fig. 5 of Hawken and Gegenfurtner (2001).

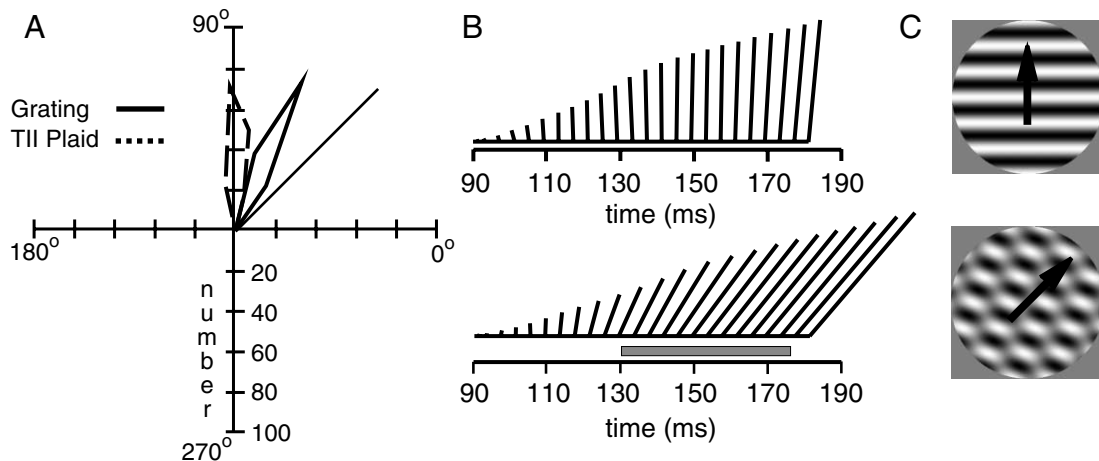


Fig. 8. Ocular following of 'uni-kinetic' plaids. The direction of the initial response is dominated by the 1D component (identical with that to a single grating drifting upwards, black arrow) but subsequently deviates towards the pattern (2D) direction, which contains a rightward component. (A) Polar histogram of the tracking directions (averaged over the time period indicated by the gray bar in B) for either a single grating moving upwards or a plaid pattern moving upward and rightward. The solid line indicates the true direction of pattern motion ( $45^\circ$ ). (B) Instantaneous mean velocity vectors to the same two stimulus types (grating, top; uni-kinetic plaid, bottom). (C) Examples of the visual stimuli used in the experiments: grating (top) and uni-kinetic plaids (bottom). Modified from fig. 9 of Masson and Castet (2002).

As shown in Fig. 3, these local motion vectors are not necessarily aligned with the direction of object motion. The second stage integrates the local motion signals into a global representation of object motion, and the third stage uses the global velocity signals to drive the eye velocity. For the most part, models of motion integration focus on the computations underlying stages one and two (Wilson and Kim, 1994; Simoncelli and Heeger, 1998; Lidén and Pack, 1999), while models of pursuit initiation are largely concerned with stages two and three (Robinson et al., 1986; Krauzlis and Lisberger, 1994). Because the second stage constitutes the output of motion integration and the input to pursuit initiation, it is of great theoretical interest in understanding the experimental findings discussed in this review.

Anatomically, the second stage is associated with MT in all of the models mentioned above. Indeed, there is compelling evidence that the responses of MT neurons are directly related to pursuit initiation (Newsome et al., 1985; Movshon et al., 1990; Groh et al., 1997) and motion integration (Movshon et al., 1986; Albright, 1991; Pack and Born, 2001). A controversial question concerns the nature of the computation by which MT neurons convert local motion signals into global representations of object motion. Recent physiological work has examined MT responses to a variety of motion stimuli, so it is now possible to place strong constraints on biological models of motion integration.

At a minimum, models of MT neurons must perform motion integration. A substantial proportion of the MT population in the alert animal responds to the global direction of object motion, rather than the local motion signals (Pack and Born, 2001; Pack et al., 2001). Furthermore, the motion integration process is not instantaneous: the early responses reflect the local motion signals, and the integrated motion signal is apparent only after 60–100 ms (Fig. 6). Given that the eye movement behavior exhibits a similar transition (Fig. 4), this property is crucial to any model of motion integration. Additionally, a motion integration system requires some type of segmentation system to prevent it from integrating motion signals from separate objects or from the background. The experiments of Recanzone and Wurtz (1999) have shown that MT neurons do indeed possess this property, and that it is at least partially under cog-

nitive control. Similarly, other experiments (Duncan et al., 2000) suggest that MT neurons can switch between integration and segmentation depending on the surface layout of the stimulus. Finally, many MT neurons encode the direction of 2nd order motion (Albright, 1992; Churan and Ilg, 2001), consistent with the finding that 2nd order motion signals drive pursuit eye movements (Lindner and Ilg, 2000; Hawken and Gegenfurtner, 2001; Fig. 7). However, Churan and Ilg (2001) also showed that MT neurons do not respond to certain stimuli that drive pursuit eye movements, such as theta motion, indicating that MT is not the final or only integration stage in the pathway.

Existing models of motion integration cover a broad range of explanations, so it is useful to evaluate them in terms of the four properties outlined above: motion integration, temporal dynamics, motion segmentation, and response to 2nd order motion. Perhaps the simplest motion integration mechanism has been proposed by Simoncelli and Heeger (1998). Here motion integration is achieved by an appropriate feedforward weighting of local motion signals. The result is a vector representing the one velocity that is most consistent with the local motion signals (Adelson and Movshon, 1982). This approach can be expected to work very well for situations in which the pursuit target is a single moving object. However, this model lacks both temporal dynamics and a motion segmentation system, and does not respond to 2nd order motion, so it would need to be substantially extended to account for the pursuit eye movement phenomena described herein. A different feedforward approach, proposed by Nowlan and Sejnowski (1995), proposes that some MT cells integrate motion signals by according greater weight to parts of the stimulus that contain veridical motion information. This mechanism would measure the velocity at features such as endpoints, intersections, and corners, where the aperture problem shown in Fig. 3 does not apply. The same mechanism could be used to perform motion segmentation, but it is not clear how the model would generate temporal dynamics, or how it would respond to 2nd order motion. Another model that explicitly tracks object features was proposed by Lidén and Pack (1999). This model consists of separate motion integration and segmentation systems that are linked within MT

by recurrent networks. The recurrent networks propagate motion signals across space, and in so doing provide a good qualitative fit to the temporal dynamics observed in MT (Pack and Born, 2001; Fig. 6C). This model has not been tested on 2nd order motion. The model of Wilson and Kim (1994) proposes an intermediate processing stage between V1 and MT that computes 2nd order motion. In model simulations, this additional route, identified with the second visual area (V2), adds a temporal delay and might account for that observed in MT. The model is also capable of motion integration and segmentation, and is therefore qualitatively capable of providing the four types of pursuit signals listed above. Finally, the model of Grossberg et al. (2001) accomplishes motion integration and segmentation, and simulates some of the phenomena that Wilson and Kim (1994) have attributed to the 2nd order pathway. This model relies on feedback connections to track image features in a manner similar to that of Lidén and Pack (1999) and with similar temporal dynamics. Each of the models predicts specific roles for the various visual areas in the primate brain, and each of these predictions is currently awaiting experimental validation.

### Conclusions

A large number of experiments using a rich variety of visual stimuli have addressed the question of how the pursuit system integrates local motion cues into a veridical representation of object motion. The major consensus is that the earliest responses are not, in fact, veridical, but represent a quick-and-dirty vector-average that serves to get the eyes moving in approximately the right direction. This initial estimate is refined over time by taking into account higher-order properties of the stimulus, such as those attributable to terminators, or by limiting the pool of motion vectors averaged through, for example, selective attention. Although a wide variety of models offer solutions as to how this refinement might be accomplished, the specific physiological mechanisms at work remain unknown. Future experiments aimed at elucidating the mechanism of integration should focus on a functional dissection of the multiple anatomical pathways by which motion information reaches MT and other pursuit-related areas.

### Acknowledgements

We thank Dr. Phillip Hendrickson for excellent technical assistance during the course of these experiments. This work was supported by NIH grants EY11379, EY12196 and RR00168 and a grant from the Whitehall Foundation.

### References

- Adelson, E.H. and Movshon, J.A. (1982) Phenomenal coherence of moving visual patterns. *Nature*, 300: 523–525.
- Albright, T.D. (1991) Color and the integration of motion signals. *Trends Neurosci.*, 14: 266–269.
- Albright, T.D. (1992) Form-cue invariant motion processing in primate visual cortex. *Science*, 255: 1141–1143.
- Beutter, B.R. and Stone, L.S. (2000) Motion coherence affects human perception and pursuit similarly. *Vis. Neurosci.*, 17: 139–153.
- Blatt, G.J., Andersen, R.A. and Stoner, G.R. (1990) Visual receptive field organization and cortico-cortical connections of the lateral intraparietal area (area LIP) in the macaque. *J. Comp. Neurol.*, 299: 421–445.
- Born, R.T. (2001) Visual processing: parallel-er and parallel-er. *Curr. Biol.*, 11: R566–R568.
- Born, R.T., Groh, J.M., Zhao, R. and Lukasewycz, S.J. (2000) Segregation of object and background motion in visual area MT: effects of microstimulation on eye movements. *Neuron*, 26: 725–734.
- Bremmer, F., Ilg, U.J., Thiele, A., Distler, C. and Hoffmann, K.P. (1997) Eye position effects in monkey cortex. I. Visual and pursuit-related activity in extrastriate areas MT and MST. *J. Neurophysiol.*, 77: 944–961.
- Carpenter, R.H.S. (1988) *Movements of the Eyes*. 2nd ed., Pion Ltd., London.
- Cavanagh, P. and Mather, G. (1989) Motion: the long and short of it. *Spat. Vis.*, 4: 103–129.
- Chubb, C. and Sperling, G. (1988) Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *J. Opt. Soc. Am. A*, 5: 1986–2007.
- Churan, J. and Ilg, U.J. (2001) Processing of second-order motion stimuli in primate middle temporal area and medial superior temporal area. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.*, 18: 2297–2306.
- Derrington, A.M. and Lennie, P. (1984) Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *J. Physiol.*, 357: 219–240.
- DeYoe, E.A. and Van Essen, D.C. (1985) Segregation of efferent connections and receptive field properties in visual area V2 of the macaque. *Nature*, 317: 58–61.
- Duncan, R.O., Albright, T.D. and Stoner, G.R. (2000) Occlusion and the interpretation of visual motion: perceptual and neuronal effects of context. *J. Neurosci.*, 20: 5885–5897.
- Dursteler, M.R. and Wurtz, R.H. (1988) Pursuit and optokinetic deficits following chemical lesions of cortical areas MT and MST. *J. Neurophysiol.*, 60: 940–965.

- Eckmiller, R. and Bauswein, E. (1986) Smooth pursuit eye movements. *Prog. Brain Res.*, 64: 313–323.
- Felleman, D.J. and Van Essen, D.C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex*, 1: 1–47.
- Ferrera, V.P. and Lisberger, S.G. (1995) Attention and target selection for smooth pursuit eye movements. *J. Neurosci.*, 15: 7472–7484.
- Ferrera, V.P. and Lisberger, S.G. (1997a) The effect of a moving distractor on the initiation of smooth-pursuit eye movements. *Vis. Neurosci.*, 14: 323–338.
- Ferrera, V.P. and Lisberger, S.G. (1997b) Neuronal responses in visual areas MT and MST during smooth pursuit target selection. *J. Neurophysiol.*, 78: 1433–1446.
- Groh, J.M., Born, R.T. and Newsome, W.T. (1997) How is a sensory map read out? Effects of microstimulation in visual area MT on saccades and smooth pursuit eye movements. *J. Neurosci.*, 17: 4312–4330.
- Grossberg, S., Mingolla, E. and Viswanathan, L. (2001) Neural dynamics of motion integration and segmentation within and across apertures. *Vision Res.*, 41: 2521–2553.
- Hawken, M.J. and Gegenfurtner, K.R. (2001) Pursuit eye movements to second-order motion targets. *J. Opt. Soc. Am. A Opt. Image Sci. Vis.*, 18: 2282–2296.
- Heinen, S.J. and Watamaniuk, S.N. (1998) Spatial integration in human smooth pursuit. *Vision Res.*, 38: 3785–3794.
- Ilg, U.J. (1997) Slow eye movements. *Prog. Neurobiol.*, 53: 293–329.
- Kawano, K. (1999) Ocular tracking: behavior and neurophysiology. *Curr. Opin. Neurobiol.*, 9: 467–473.
- Kawano, K., Shidara, M., Watanabe, Y. and Yamane, S. (1994) Neural activity in cortical area MST of alert monkey during ocular following responses. *J. Neurophysiol.*, 71: 2305–2324.
- Keller, E.L. and Heinen, S.J. (1991) Generation of smooth-pursuit eye movements: neuronal mechanisms and pathways. *Neurosci. Res.*, 11: 79–107.
- Komatsu, H. and Wurtz, R.H. (1988) Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J. Neurophysiol.*, 60: 580–603.
- Komatsu, H. and Wurtz, R.H. (1989) Modulation of pursuit eye movements by stimulation of cortical areas MT and MST. *J. Neurophysiol.*, 62: 31–47.
- Kowler, E. and McKee, S.P. (1987) Sensitivity of smooth eye movement to small differences in target velocity. *Vision Res.*, 27: 993–1015.
- Krauzlis, R.J. and Lisberger, S.G. (1994) A model of visually guided smooth pursuit eye movements based on behavioral observations. *J. Comput. Neurosci.*, 1: 265–283.
- Lamme, V.A., Super, H. and Spekreijse, H. (1998a) Feedforward, horizontal, and feedback processing in the visual cortex. *Curr. Opin. Neurobiol.*, 8: 529–535.
- Lamme, V.A., Zipser, K. and Spekreijse, H. (1998b) Figure-ground activity in primary visual cortex is suppressed by anesthesia. *Proc. Natl. Acad. Sci. USA*, 95: 3263–3268.
- Levitt, J.B., Kiper, D.C. and Movshon, J.A. (1994a) Receptive fields and functional architecture of macaque V2. *J. Neurophysiol.*, 71: 2517–2542.
- Levitt, J.B., Yoshioka, T. and Lund, J.S. (1994b) Intrinsic cortical connections in macaque visual area V2: evidence for interaction between different functional streams. *J. Comp. Neurol.*, 342: 551–570.
- Lidén, L. and Pack, C. (1999) The role of terminators and occlusion cues in motion integration and segmentation: a neural network model. *Vision Res.*, 39: 3301–3320.
- Lindner, A. and Ilg, U.J. (2000) Initiation of smooth-pursuit eye movements to first-order and second-order motion stimuli. *Exp. Brain Res.*, 133: 450–456.
- Lisberger, S.G. and Ferrera, V.P. (1997) Vector averaging for smooth pursuit eye movements initiated by two moving targets in monkeys. *J. Neurosci.*, 17: 7490–7502.
- Lisberger, S.G. and Movshon, J.A. (1999) Visual motion analysis for pursuit eye movements in area MT of macaque monkeys. *J. Neurosci.*, 19: 2224–2246.
- Lisberger, S.G. and Westbrook, L.E. (1985) Properties of visual inputs that initiate horizontal smooth pursuit eye movements in monkeys. *J. Neurosci.*, 5: 1662–1673.
- Lisberger, S.G., Morris, E.J. and Tychsen, L. (1987) Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annu. Rev. Neurosci.*, 10: 97–129.
- Lorençeau, J., Shiffrar, M., Wells, N. and Castet, E. (1993) Different motion sensitive units are involved in recovering the direction of moving lines. *Vision Res.*, 33: 1207–1217.
- Mack, A., Fendrich, R. and Pleune, J. (1979) Smooth pursuit eye movements: is perceived motion necessary?. *Science*, 203: 1361–1363.
- Mareschal, I. and Baker Jr., C.L. (1998) Temporal and spatial response to second-order stimuli in cat area 18. *J. Neurophysiol.*, 80: 2811–2823.
- Masson, G.S. and Castet, E. (2002) Parallel motion processing for the initiation of short-latency ocular following in humans. *J. Neurosci.*, in press.
- Masson, G.S. and Stone, L.S. (2002) From following edges to pursuing objects. *J. Neurophysiol.*, in press.
- Masson, G.S., Rybarczyk, Y., Castet, E. and Mestre, D.R. (2000) Temporal dynamics of motion integration for the initiation of tracking eye movements at ultra-short latencies. *Vis. Neurosci.*, 17: 753–767.
- Maunsell, J.H. and Van Essen, D.C. (1983) The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey. *J. Neurosci.*, 3: 2563–2586.
- Merigan, W.H., Nealey, T.A. and Maunsell, J.H. (1993) Visual effects of lesions of cortical area V2 in macaques. *J. Neurosci.*, 13: 3180–3191.
- Morris, E.J. and Lisberger, S.G. (1987) Different responses to small visual errors during initiation and maintenance of smooth-pursuit eye movements in monkeys. *J. Neurophysiol.*, 58: 1351–1369.
- Movshon, J.A., Adelson, E.H., Gizzi, M.S. and Newsome, W.T. (1986) The analysis of moving visual patterns. In: C. Chagas, R. Gattass and C. Gross (Eds.), *Pattern Recognition Mechanisms*. Springer, New York, pp. 117–151.
- Movshon, J.A., Lisberger, S.G. and Krauzlis, R.J. (1990) Visual

#2

#3

- cortical signals supporting smooth pursuit eye movements. *Cold Spring Harb. Symp. Quant. Biol.*, 55: 707–716.
- Newsome, W.T., Wurtz, R.H., Dursteler, M.R. and Mikami, A. (1985) Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *J. Neurosci.*, 5: 825–840.
- Nowlan, S.J. and Sejnowski, T.J. (1995) A selection model for motion processing in area MT of primates. *J. Neurosci.*, 15: 1195–1214.
- Pack, C.C. and Born, R.T. (2001) Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature*, 409: 1040–1042.
- Pack, C.C., Berezovskii, V.K. and Born, R.T. (2001) Dynamic properties of neurons in cortical area MT in alert and anaesthetized macaque monkeys. *Nature*, 414: 905–908.
- Rashbass, C. (1961) The relationship between saccadic and smooth tracking eye movements. *J. Neurophysiol.*, 159: 326–338.
- Recanzone, G.H. and Wurtz, R.H. (1999) Shift in smooth pursuit initiation and MT and MST neuronal activity under different stimulus conditions. *J. Neurophysiol.*, 82: 1710–1727.
- Recanzone, G.H. and Wurtz, R.H. (2000) Effects of attention on MT and MST neuronal activity during pursuit initiation. *J. Neurophysiol.*, 83: 777–790.
- Robinson, D.A., Gordon, J.L. and Gordon, S.E. (1986) A model of the smooth pursuit eye movement system. *Biol. Cybern.*, 55: 43–57.
- Saito, H., Yukiie, M., Tanaka, K., Hikosaka, K., Fukada, Y. and Iwai, E. (1986) Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J. Neurosci.*, 6: 145–157.
- Shipp, S. and Zeki, S. (1989) The organization of connections between areas V5 and V2 in macaque monkey visual cortex. *Eur. J. Neurosci.*, 1: 333–354.
- Simoncelli, E.P. and Heeger, D.J. (1998) A model of neuronal responses in visual area MT. *Vision Res.*, 38: 743–761.
- Watamaniuk, S.N. and Heinen, S.J. (1999) Human smooth pursuit direction discrimination. *Vision Res.*, 39: 59–70.
- Williams, D.W. and Sekuler, R. (1984) Coherent global motion percepts from stochastic local motions. *Vision Res.*, 24: 55–62.
- Wilson, H.R. and Kim, J. (1994) A model for motion coherence and transparency. *Vis. Neurosci.*, 11: 1205–1220.
- Wilson, H.R., Ferrera, V.P. and Yo, C. (1992) A psychophysically motivated model for two-dimensional motion perception. *Vis. Neurosci.*, 9: 79–97.
- Yabuta, N.H., Sawatari, A. and Callaway, E.M. (2001) Two functional channels from primary visual cortex to dorsal visual cortical areas. *Science*, 292: 297–300.

QUERIES:

?#1: Is this is the appropriate location for ref. to Fig. 2? (page 227)

?#2: Update? (page 236)

?#3: Update? (page 236)