Tracking with the mind’s eye

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The two components of voluntary tracking eye-movements in primates, pursuit and saccades, are generally viewed as relatively independent oculomotor subsystems that move the eyes in different ways using independent visual information. Although saccades have long been known to be guided by visual processes related to perception and cognition, only recently have psychophysical and physiological studies provided compelling evidence that pursuit is also guided by such higher-order visual processes, rather than by the raw retinal stimulus. Pursuit and saccades also do not appear to be entirely independent anatomical systems, but involve overlapping neural mechanisms that might be important for coordinating these two types of eye movement during the tracking of a selected visual object. Given that the recovery of objects from real-world images is inherently ambiguous, guiding both pursuit and saccades with perception could represent an explicit strategy for ensuring that these two motor actions are driven by a single visual interpretation.
REVIEW

Although there are clear distinctions between a wider range of difficult real-world problems and natural primate eye-movements confront and solve a much greater deal has been learned by tracking single-spot stimuli, error signal used to drive the eyes. Although a great deal of work has been done on the circuits for eye movements can be largely described as feedback systems in which retinal-based information is interpreted as an error signal to drive the eyes. Furthermore, older studies found combined pursuit- and saccade-related responses in regions traditionally considered to be components of the pursuit system, such as the ventral PF (Ref. 16) and the major target of the ventral PF, the vestibular nuclei (Ref. 17). Finally, the simplicity of the conventional pathway for pursuit suggested in Fig. 1 is further questioned by recent anatomical data showing that the major target of visual projections from the pons is the dorsal PF, as opposed to the ventral PF (Ref. 20). The dorsal PF, in turn, projects to eye-movement-related regions in the interpositus and dentate cerebellar nuclei, which provide feedback projections to the W. and, via the thalamus, to the cerebral cortex. Although there are clear distinctions between the properties of pursuit and saccades, these findings show that there are multiple overlapping routes through which these two systems might share sensory information and coordinate motor output. The wiring diagram outlined in Fig. 1 might appear to be overly complex for such apparently simple movements. In typical oculomotor studies, observers track a single spot of light moving over a featureless background in an otherwise completely dark room. These studies have explored the basic premise that the circuits for eye movements can be largely described as feedback systems in which retinal-based information is interpreted as an error signal to drive the eyes. Although a great deal has been learned by tracking single-spot stimuli, primate eye-movements confront and solve a much wider range of difficult real-world problems. Natural environments typically contain multiple stationary and moving objects, any of which might also be partially hidden. Consequently, the sequence of retinal images that typically occurs during normal behavior is much more complex than that produced by the oculomotor scientist’s classical spot. Visual perception relies on the

Fig. 1. An outline of the neural pathways for pursuit and saccades. The gray shaded regions indicate general brain structures and the boxes indicate specific brain regions. The major pathways traditionally hypothesized for pursuit (blue) and saccades (red) are highlighted. Solid lines with arrows illustrate the anatomical connections between the regions indicated by each box; the broken line with arrow indicates the physical link between the eye and the retina. Within the cerebellum, broken lines within broken separate cortical regions from their associated target nuclei. For clarity, some closely related regions are grouped within a single box. Abbreviations: FEF, frontal eye fields; LGN, lateral geniculate nucleus; LIP, lateral intraparietal area; MD, mediodorsal nucleus; MN, oculomotor nuclei; MST, medial superior temporal area; MT, middle temporal area; NRT, nucleus reticularis tegmenti pontis; PF, paraflocculus; PH, nucleus prepositus hypoglossi; PN, basilar pontine nuclei; PPRF, paramedian pontine reticular formation; RiMLF, rostral interstitial nucleus of the medial longitudinal fasciculus; SC, superior colliculus; SNr, substantia nigra pars reticulata; V1, primary visual cortex; VL, ventrolateral nucleus; VN, vestibular nuclei.

Likewise, the vermis in the cerebellum and one of its major inputs from the pons, the nucleus reticularis tegmenti pontis, has been shown to be involved in both pursuit and saccades. Conversely, older studies found combined pursuit- and saccade-related responses in regions traditionally considered to be components of the pursuit system, such as the ventral PF (Ref. 16) and the major target of the ventral PF, the vestibular nuclei. Finally, the simplicity of the conventional pathway for pursuit suggested in Fig. 1 is further questioned by recent anatomical data showing that the major target of visual projections from the pons is the dorsal PF, as opposed to the ventral PF (Ref. 20). The dorsal PF, in turn, projects to eye-movement-related regions in the interpositus and dentate cerebellar nuclei, which provide feedback projections to the W. and, via the thalamus, to the cerebral cortex. Although there are clear distinctions between the properties of pursuit and saccades, these findings show that there are multiple overlapping routes through which these two systems might share sensory information and coordinate motor output.

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Fig. 2. Shared motion integration for perception and pursuit. The sinusoidal oblique object motion (at angles ±10° from straight down) of a line-figure diamond was viewed through two vertical apertures such that the only motion displayed was that of four oblique line-segments moving up and down. The broken black lines indicate the completed object, but these lines were never visible. The identical object and segment motion produces two different percepts depending on the luminance of the apertures. This figure shows the raw eye-position trajectories for ±10° (red) and ±15° (blue) object motion for two aperture conditions. (A) Dark visible apertures produce a percept of the coherent oblique motion of the diamond. Under these conditions, pursuit follows the object motion (±6.8° and ±11.0° for the red and blue traces, respectively). (B) Equiluminant invisible apertures (indicated in the figure by broken white lines that were not present in the stimulus) produce an incoherent percept of four independent line-segments. Under these conditions, pursuit follows the vertical motion of the segments (±0.5° and ±2.6°, respectively).
ability of the visual system to infer the 3D spatial location and motion of real objects from the ambiguous 2D patterns of luminance changes on the retina. The brain must segment the image into objects, and reconstruct the third dimension of depth from incomplete sensory information. The solutions to these problems are generally not unique: either a priori knowledge or additional assumptions about the world and the types of objects and motions that one is likely to encounter are needed to resolve the inherent ambiguity of retinal images.

This article will review evidence that the complexity and interconnectivity of the pathways for pursuit and saccades is related to two important issues: (1) the need to produce eye movements in response to the real-world objects that one perceives, rather than to the raw retinal signals; and (2) the need to coordinate pursuit and saccades by using a shared representation of the visual scene, rather than by driving the two movements with independent and potentially conflicting interpretations. Furthermore, the view that the input for tracking eye movements is closely related to the visual perception of target location and motion in the world invites a reinterpretation of the function of the output pathways and, in particular, a reassessment of the role of the cerebellum.

The driving force for tracking eye movements: retinal versus perceived stimuli

For some time, it has been widely accepted that saccades are not guided by the raw retinal stimulus, but rather by a higher-order representation of target spatial location. For example, if subjects are briefly shown a pair of spots at different locations, they can make an accurate sequence of saccades to each remembered location, even though both spots are extinguished before the first saccade is completed. This indicates that saccades are guided by the remembered spatial coordinates of the stimuli, rather than by their retinal locations. Recent search studies have shown that both saccadic and perceptual target localization are similarly affected by target salience and have similar detection accuracies. Furthermore, saccades and perception can also be fooled by the same tricks. A moving background induces an illusory displacement of the target location (the ‘Duncker illusion’) and a matching displacement of the saccadic endpoint, suggesting that saccades are guided by the erroneously perceived location, rather than the retinal retinal location. Finally, studies have provided evidence that the preparation of saccades is coupled to the control of attention and that these mechanisms involve the same brain regions.

Unlike saccades, pursuit is not generally acknowledged to be guided by perception. The current computational models of pursuit (for examples, see Refs 34, 35) assume, at least tacitly, that raw retinal-image motion, which is independent of perception, is the controlled variable. Although there is a history of challenges to this assumption, earlier findings that suggested a link between perception and pursuit were not conclusive: (1) the tracking of retinal stimuli, which generates the perception of motion without any retinal motion, could simply reflect a small response to position inputs amplified by pursuit feedback. (2) Perceptual enhancements of smooth eye responses during head movements caused by the presence of a foveal afterimage could simply reflect an attentional enhancement of the vestibulo-ocular reflex; and (3) changes in the pursuit of an electronically stabilized target associated with illusory changes in target motion simply reflect deviations from the natural-control strategy induced by sustained stabilization of a pursuit response in the perceived direction and an optokinetic response in the direction of the inducer. Steinbach provides important evidence that pursuit can follow a moving object that has no obvious retinal counterpoint. He showed that humans generate large illusory changes in perceived object motion in response to the perceived horizontal motion of a rolling wagon wheel that is defined only by the cycloidal motions of points fixed to its circumference. Unfortunately, the centroid of these points also moved horizontally so the observed pursuit could simply have been a response to a low-spatial-frequency elementary motion detector, without the need for any higher-order perceptually related visual processing. More recently, a clear quantitative correlation between perceptual and pursuit performance was demonstrated using line-figure objects viewed through vertical apertures (Fig. 2). Such partially occluded stimuli can be used to induce changes in perceived motion and pursuit without any alteration of the image motion. Furthermore, unlike spots, they produce sustained retinal-image motion that is different from the underlying object motion even during steady-state pursuit. When the object motion of a line-figure stimulus is perceived as coherent because of the compelling sense of occlusion provided by dark visible apertures, pursuit can follow the oblique motion of the object (Fig. 2A). When the apertures are made identical to the background, so as to break up the percept of a single moving object, pursuit follows the vertical motion of the individual line segments (Fig. 2B). Another recent experiment presented a moving rectangular aperture that contained moving dots. By moving the dots in the direction opposite to that of the aperture, the retinal image motion of the dots was pitted directly against the object motion of the aperture. This fact that humans can follow such an object smoothly demonstrates that perceived object motion can override even contradictory retinal-motion cues. Another recent study has shown that smooth-vergence eye-movements, which might be thought of as pursuit in depth, can track changes in illusory perceived depth (the kinetic depth effect) without any change in binocular disparity. Finally, a study examining perception during pursuit has provided evidence that the same attentional filter modulates both perception and pursuit.

Although the correlation between perceived object motion and pursuit behavior is strong, one could argue that both are largely vertical and that the performance similarities arise as a consequence of separate mechanisms that arrive at the same answer. Several recent studies show that pursuit and perception are both influenced by the same factors that produce erroneous or biased responses. The unique perceptual analyses derived from eye-movement data, together with standard psychometric functions, makes it possible to compare the errors in perceptual and pursuit performance.
Physiological studies corroborate the idea that both forms of voluntary tracking eye-movements share cortical processing that is related to perception. Stimulation and lesions of the MT and the MST areas affect both motion perception and pursuit. Lesions of MT also provide irrefutable evidence for the overlap of visual processing for saccades and pursuit; they not only produce pursuit deficits, but also saccadic errors to moving targets, consistent with the loss of a shared motion input.

Neurons in MST exhibit sustained responses during pursuit, even if the target object is retinally stabilized, briefly “blinking” off, or if its motion is only implied or imagined. Thus, both retinal and non-retinal motion information are combined in MST to generate a neural signal that supports both pursuit and perception, and that appears to encode information about the motion of the object in the world. Studies of the adjacent posterior parietal cortex, such as area LIP, demonstrate an important role in both spatial perception and saccadic programming. In a recent study using the Duncker illusion, LIP neurons were found to encode the location of the future erroneous saccade, consistent with the illusory perceptual mislocalization and inconsistent with the retinal location of the target.

**Internal positive feedback for pursuit: velocity memory versus plant compensation**

How might the perceptual signals described in the previous section be used to generate the motor commands that guide pursuit and saccades? For saccades, we have a detailed understanding of how different classes of subcortical neurons participate in generating the motor burst required to rotate the eyes quickly. For pursuit, the motor circuitry is less clear, although details have emerged over the past two decades that suggest how the brainstem and cerebellum might form the pursuit motor command. Because the retina is linked mechanically to the moving eye, pursuit is constrained physically by negative feedback. As such, accurate steady-state pursuit of a small spot is impossible without an extra-retinal signal, because the generation of perfect pursuit necessarily eliminates the retinal-image motion that provides the sensory input for pursuit. Therefore, it has been suggested that internal positive feedback of an eye-velocity signal might be used to sustain steady-state pursuit. A number of physiological studies found considerable support for positive feedback through the cerebellum that could serve as an eye-velocity memory for pursuit. More specifically, Purkinje cells in the ventral PF receive pursuit-related input and maintain their pursuit-related output during sustained steady-state pursuit, even in the absence of any residual image motion. By updating the activity within this positive-feedback loop with descending visual information about residual retinal motion, the output of the ventral PF could continuously provide a command signal that is related to the current eye speed, plus any necessary corrective eye accelerations.

However, the evidence described in the previous section, that cortical areas directly provide an object-motion signal as the input for pursuit, suggests a different control strategy. If information about visual motion and eye motion is already combined in the cerebral cortex, there is no need to combine them downstream in the brainstem–cerebellar pathways. However, the presence of sustained activity at the level of the cerebellum during steady-state pursuit might simply reflect the sustained activity of an input from MST (Ref. 55). An alternative role for the cerebellar eye-velocity signal has been corroborated by recent studies of the ventral
Facilitation, and saccades, it is unclear whether these effects reflect a single process or simply independent processes. However, because it would be maladaptive to track one object with pursuit and another with saccades, it would be highly advantageous if the selection of the target object were shared by pursuit and saccades. This hypothesis finds some support in the recent finding that the early extinction of a fixed stimulus produces parallel decreases in the latency of saccades and pursuit to a second stimulus (the ‘gap effect’). Even if the selection process is shared, the target object is nonetheless linked to multiple attributes (for example, its location, velocity or shape), which could have differentially weighted effects on saccades and pursuit. For example, because motion is more important to pursuit than location, and the converse is true for saccades, resource allocation to a specific attribute, such as location, might be expected to produce qualitatively different effects on the two types of eye movement. Indeed, preliminary data suggest that when observers are given prior information about the location of an upcoming target, although the latencies of both saccades and pursuit are decreased, the effects on saccades are larger.

The possible neural mechanisms that underlie the selection process are only beginning to be understood. In the SC, eye-movement-related neurons exhibit graded responses that might encode the probability that the stimulus in the response field is the target from a priori information or from a posteriori analysis of the sensory cue to target location information available to both small saccades and pursuit. Several cortical areas also appear to be influenced by or to participate in target selection. Saccade-related neurons in FEW and LIP respond more strongly when the stimulus in the response field is a target or behaviorally relevant than when it is a distractor or irrelevant. Furthermore, the latency of eye-movement-related activity in FEW is appropriate for regulating the decision of when to initiate or cancel a saccade, and appears to be linked to salience-induced differences in perceptual

Coordination of pursuit and saccades: target selection and motor decisions

In addition to segmenting the visual scene into objects, the brain must also decide how to allocate visual resources between those objects. Because eye movements determine which objects will be foveated and visually stabilized, voluntary saccades and pursuit should reflect the process of selecting one target from the various candidates within the visual scene. Indeed, several studies have shown that the latency of saccades increases when observers must select the visual field for a unique target among a set of stimuli, and does so in direct relation to the difficulty in finding the target. Similar increases in latency have been observed for pursuit when an observer must choose between two stimuli moving in opposite directions. While such latency effects suggest that a target-selection process precedes both pursuit and saccades, it is unclear whether these effects reflect a single process or simply independent processes. However, because it would be maladaptive to track one object with pursuit and another with saccades, it would be highly advantageous if the selection of the target object were shared by pursuit and saccades. This hypothesis finds some support in the recent finding that the early extinction of a fixed stimulus produces parallel decreases in the latency of saccades and pursuit to a second stimulus (the ‘gap effect’). Even if the selection process is shared, the target object is nonetheless linked to multiple attributes (for example, its location, velocity or shape), which could have differentially weighted effects on saccades and pursuit. For example, because motion is more important to pursuit than location, and the converse is true for saccades, resource allocation to a specific attribute, such as location, might be expected to produce qualitatively different effects on the two types of eye movement. Indeed, preliminary data suggest that when observers are given prior information about the location of an upcoming target, although the latencies of both saccades and pursuit are decreased, the effects on saccades are larger.

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reaction time during search\(^{39}\). Finally, in MT and MST, neurons exhibit stronger responses for pursuit targets or behaviorally relevant motion stimuli\(^{34}\).

The suggestion that pursuit and saccades are guided by a common selection process and common estimates of object motion and location implies that the final motor decision to make a specific combination of pursuit and saccadic eye-movements occurs at a later stage. This idea has received some support from recent experiments applying microstimulation within the cerebellar motor decision to make a specific combination of pursuit and saccadic eye-movements occurs at a later stage. This idea has received some support from recent experiments applying microstimulation within the cerebellum. As the strength of microstimulation was increased, the elicited eye-movements changed abruptly from pursuit-like to saccade-like. These results suggest that the vermis in this motor decision could be mediated by projections to brainstem nuclei (such as the SC or the riMLF), which have also been implicated recently in the control of pursuit\(^{40}\) in addition to their traditional roles in the control of saccades\(^{2}\). Although firm conclusions cannot be drawn from these preliminary findings, they nonetheless indicate that there is much left to be learned about how and where the decision to generate either a smooth or saccadic eye-movement response takes place.

Dejà vu all over again

The proposal of shared visual processing for saccades and pursuit is similar to some of the ‘old’ views that were held before the current dogma about oculomotor vision. As an extension of the distinction between the ventral and dorsal vision streams, it proposes that pursuit and saccadic eye-movements are accomplished jointly by a cascade of processes that analyze and segment the retinal image, and then group the image elements into objects, estimate the location and velocity of objects in the world, and decide continuously on the appropriate motor responses. Indeed, because most actions in natural situations require synergy across multiple motor outputs, perception could have evolved to ensure that each motor component is guided by information derived from the same interpretation of the visual scene.

Selected references

37. Vorst, S. and Young, L.R. (1975) Science 190, 986–988
Sensing effectors make sense

Angela Wenning

‘Housekeepers’ of living organisms maintain salt and water balance, monitor blood sugar and schedule their work to the season and the time of day in order to perform their chores, they rely on information about the status quo. The traditional concept of a sensor that communicates with a central comparator authorizing an effector, which was inspired by engineers, has become blurred in the search for morphological correlates of such regulatory cascades. In many cases, neurons, which are both sensory and neurosecretory, and endocrine cells equipped with smart detectors, reliably regulate autonomous functions by using local rather than central computing. Like the well-trained staff of a smoothly run household, such ‘sensing effectors’ translate information into action. Trends Neurosci. (1999) 22, 550–555

O VER THE PAST TWO DECADES, we have made significant advances in our understanding of the cellular and molecular bases of behaviour, both at the level of the processing of sensory information (for example, vision, hearing, smell and taste) and the generation of motor programs (for example, feeding, heart-beat, locomotion and vocalization). Insights into how organisms maintain their internal environment so that they are able to stay fit to execute, behavior are equally important for our understanding. Research over the past few years has shown that both afferent and efferent neurons, which are termed ‘sensing effectors’, process information and take appropriate action: for example, monitor and adjust blood-sugar levels, external osmolarity and ion levels, and tune the activity of multiple target organs according to the time and season. The concept of cells that are intrinsically sensitive to the parameter they are regulating extends to non-neural effectors, which provide information from the internal to multiple target organs according to the time and season. The concept of cells that are intrinsically sensitive to the parameter they are regulating extends to non-neural effectors, which provide information from the internal

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