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.

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WHEN VIEWING their visual surroundings, primates use a combination of saccadic and smooth-pursuit eye-movements in order to center and stabilize the retinal images of objects of interest. Saccades are discrete movements that quickly direct the eyes towards a visual target, thereby moving the image of the target from an eccentric location to the high-acuity region of the central retina, the fovea. In contrast, pursuit is a continuous eye-movement that smoothly rotates the eyes to compensate for any motion of the target. While all mammals can generate saccades and smooth optokinetic eye-movements, which track the motion of the entire visual surround, only primates can use both pursuit and saccades to track a small moving object within a complex visual scene, regardless of motion elsewhere in the visual field. The evolutionary onset of this ability coincides with the advent of a wealth of new extrastriate visual areas and a massive projection from these areas to subcortical regions (Fig. 1).

Pursuit and saccades have been viewed as largely independent oculomotor subsystems that overlap primarily at the earliest stages of the visual pathways [the retina, lateral geniculate nucleus (LGN) and primary visual cortex (V1)], and at the final stages of the oculomotor pathways [the nucleus prepositus hypoglossi (PH) and motoneurons (MN)]. The argument for segregation relies on the observation that certain brainstem lesions appear to abolish saccades selectively, while leaving pursuit intact[1]. The conventional pursuit pathways[2,3] start with the middle temporal (MT) and medial superior temporal (MST) areas, which provide the target-motion signals needed to guide pursuit. These cortical areas project to visuomotor nuclei in the pons (PN), which, in turn, project to the floccular region of the cerebellum, including the ventral paraflocculus (PF). The ventral PF drives pursuit via its projections to the vestibular nucleus (VN), which has direct access to the final motor nuclei. The conventional saccadic pathways[2] include the frontal eye fields (FEF) and lateral intraparietal area (LIP) of the cerebral cortex, the basal ganglia (for example, the caudate nucleus and the substantia nigra), and the superior colliculus (SC). These regions interact to provide the necessary target-position signals to premotor circuitry in the brainstem, including the paramedian pontine reticular formation (PPRF) and the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF), which, in turn, project to the final motor nuclei.

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Several findings cast doubt on this tidy segregation of the pathways for pursuit from those for saccades. First, close inspection of the results from lesion experiments shows that small brainstem lesions in humans and monkeys can result in deficits of large saccades, with relative sparing of both pursuit and small saccades[1,4]. Larger lesions, which are still restricted to PPRF, result in a conjugate gaze palsy that affects both saccades and pursuit[5]. Thus, the results from these experiments actually provide evidence for functional overlap between pursuit and small saccades, although they do suggest that the control of pursuit and large saccades might be segregated. Second, the distinction between pursuit-related and saccade-related areas within the cerebral cortex is less clear given the recent finding that FEF, LIP and MST each contain adjacent or overlapping subregions for pursuit and saccades[6]. For example, MT and MST are generally acknowledged to accomplish the visual motion processing that is crucial for driving pursuit, but lesions in these areas also alter the metrics of saccades to moving targets[7], and microstimulation of these areas delays the onset of saccades to stationary targets[8]. The binary distinction of cortical areas as either pursuit- or saccade-related might, therefore, be an oversimplification based on the relative importance of the sensory information processed within these areas (for example, MT and MST are deemed pursuit-related areas because motion is more important for pursuit), rather than a true dichotomy based on motor output. Third, recent studies have shown that regions in the brainstem and cerebellum that are traditionally considered components of one subsystem, are also involved in the other. Single-unit-recording and microstimulation studies indicate that the rostral portion of the SC is involved not only with small saccades and fixation, but with pursuit as well[9,10]. Furthermore, preliminary data indicate that many burst neurons in the riMLF of the cat fire during both saccades and pursuit[11].

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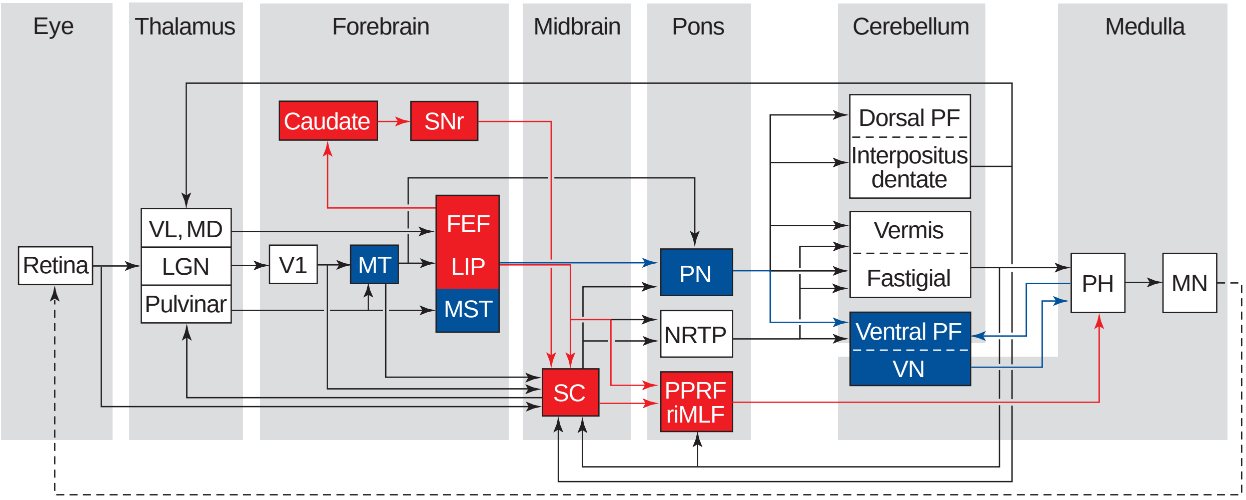

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Fig. 1. ***An outline of the neural pathways for pursuit and saccades.*** *The gray shaded regions indicate general brain structures and the boxes indicate specific brain regions. The major pathways traditionally hypothesized for pursuit (blue) and 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 boxes 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; NRTP, 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[12–15]. 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[17–19]. 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[21], which provide feedback projections to the SC and, via the thalamus, to the cerebral cortex[22,23]. 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 used to drive the eyes[24]. 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[25,26]. 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

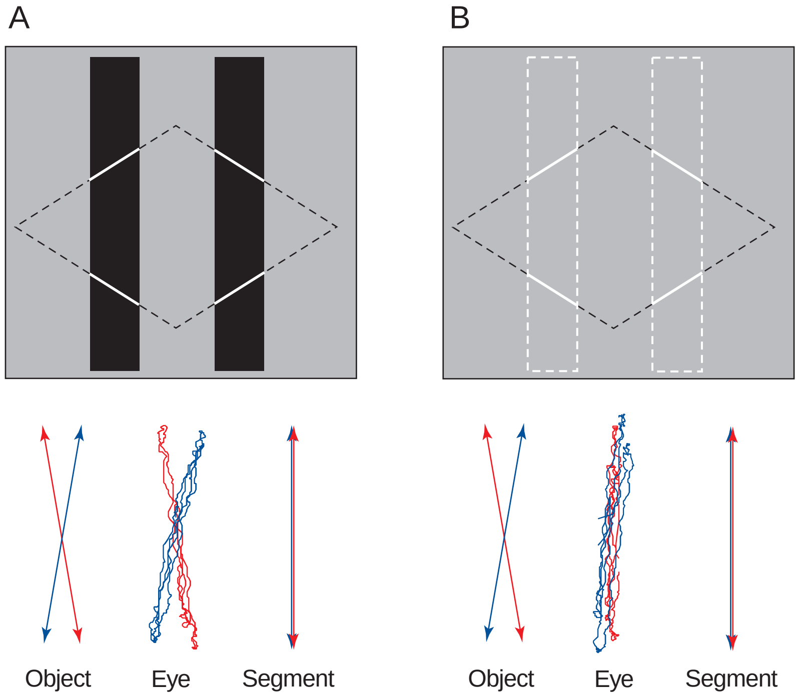

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Fig. 2. ***Shared motion integration for perception and pursuit.*** *The sinusoidal oblique object motion (at angles ±10° from straight down) of a line-figure diamond was viewed through two vertical apertures such that the only motion displayed was that of four oblique line-segments moving up and down[41]. 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[42]. This figure shows the raw eye-position trajectories for +10° (red) and −10° (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 oblique 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 locations 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 interpretation 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[27]. 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[28,29]. 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 veridical retinal location[30]. Finally, studies have provided evidence that the preparation of saccades is coupled to the control of attention[31,32] and that these mechanisms might involve the same brain regions[33].

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 afterimages[36], which generates the perception of motion without any retinal motion, could simply reflect a small response to position inputs amplified by positive 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[37]; and (3) changes in the pursuit of an electronically stabilized target associated with illusory changes in target motion[38] could simply reflect deviations from the natural-control strategy induced by sustained stabilization or a response to the added retinal motion used to generate the illusion. Similarly, early findings that purported to refute the link between perception and pursuit were equally inconclusive: the apparent absence of a pursuit movement in the direction of illusory induced motion[39] could be due to the fact that the observed movement was not simply pursuit, but the sum of a pursuit response in the perceived direction and an optokinetic response in the direction of the inducer.

Steinbach[40] provided the first direct, albeit qualitative, evidence that pursuit can follow a moving object that has no obvious retinal counterpart. He showed that humans generate largely horizontal pursuit 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[41,43]. 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[44]. The fact that humans can follow such an object smoothly demonstrates that perceived object motion can override even contradictory foveal retinal-image motion. 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[45]. Finally, a study examining perception during pursuit has provided evidence that the same attentional filter modulates both perception and pursuit[46].

Although the correlation between perceived object motion and pursuit behavior is strong, one could argue that both are largely veridical and that the performance similarities arise as a consequence of separate mechanisms that arrive at the same correct answer. However, recent studies show that pursuit and perception are both influenced by the same factors that produce erroneous or biased responses. The use of oculometric functions derived from eye-movement data, together with standard psychometric functions, makes it possible to compare the errors in perceptual and pursuit performance directly and quantitatively (Fig. 3). By applying this technique, it has been demonstrated that manipulations of aperture shape can produce similar systematic errors in the directions of both perceived motion (Fig. 3A) and of the smooth eye-movement response (Fig. 3B)[47]. Similarly, a cognitive expectation, caused by an *a priori* cue that is generally but not always correct, produces similar biases in both the perceived (Fig. 3C) and pursued (Fig. 3D) directions[48]. These studies show that pursuit and perception are fooled by the same tricks to the same degree, providing further evidence for the existence of a shared neural mechanism. Thus, the relationship between perception and pursuit mirrors that between perception and saccades, and is consistent with the view that overlapping visual pathways guide both pursuit and saccades.

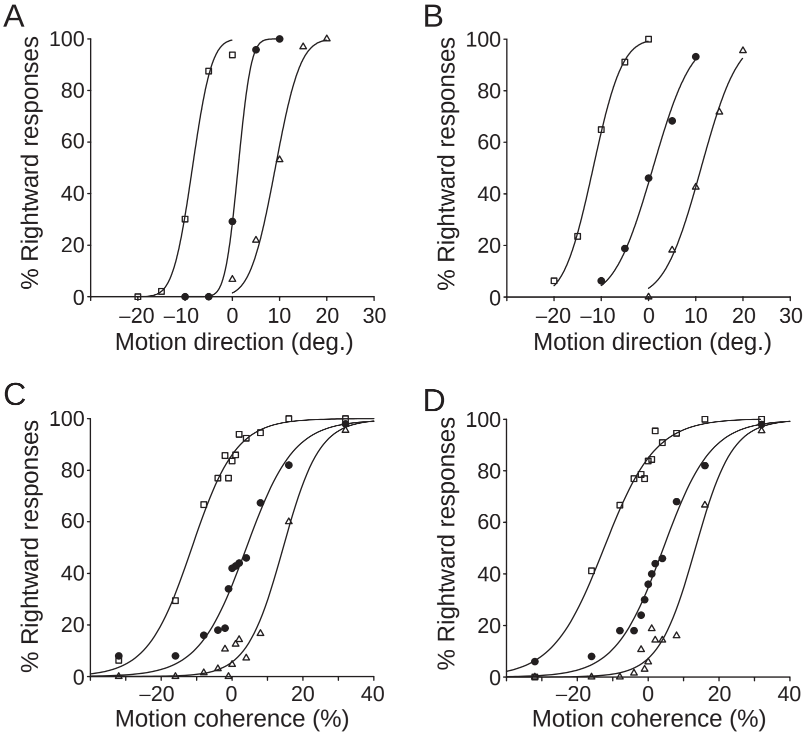

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Fig. 3. ***Shared perceptual and cognitive biases for perception and pursuit.*** **(A)** *Three psychometric curves of an observer asked to judge the direction of motion of a moving plaid (left–right judgment with respect to straight down) as a function of the actual direction of motion[47]. The judgments were made under three conditions: (1) with an elongated window tilted 40° to the right (open squares) that produced a rightward bias and, therefore, a leftward shift; (2) with a circularly symmetric window (filled circles) that produced no bias; and (3) with an elongated window tilted 40° to the left (open triangles) that produced a leftward bias and therefore a rightward shift. For perception, the point of subjective downward (PSD) was −9.1°, −1.2° and +8.5° for the right-tilted, symmetrical and left-tilted apertures, respectively.* **(B)** *Three oculometric curves (a measure of the pursuit response) for the same observer, same set of trials and same three conditions. For pursuit, the PSD was −11.1°, −0.9° and +11.7° for the right-tilted, symmetrical and left-tilted apertures, respectively.* **(C)** *Three psychometric curves of an observer asked to judge the direction (left–right) of random dot motion as a function of the fraction of displayed dots moving in the same direction (also called 'motion coherence)[7,48]. The judgments were made under three conditions: (1) with the stimulus preceded by a cue indicating that the upcoming motion was likely to be righward (open squares) and, thus, produced a rightward bias and leftward shift; (2) with no cue (filled circles); and (3) with a leftward cue (open triangles) that produced a leftward bias and a rightward shift. For perception, the points of subjective equality (PSEs) were −11%, +4% and +14% for the rightward-cue, no-cue and leftward-cue conditions, respectively.* **(D)** *Three oculometric curves for the same observer on the same trials. For pursuit, the PSEs were −12%, +4% and +13% for the rightward-cue, no-cue and leftward-cue conditions, respectively.*

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[7,8,49–54]. 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[7]. Neurons in MST exhibit sustained responses during pursuit, even if the target object is retinally stabilized, briefly 'blinked' off, or if its motion is only implied or imagined[55,56]. 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[57,58]. 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[59].

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[60]. 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[3]. 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[37,61]. A number of physiological studies found considerable support for positive feedback through the cerebellum that could serve as an eye-velocity memory for pursuit[61,62]. 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[63]. 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[3,63,64].

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. In particular, the presence of sustained activity at the level of the cerebellum during steady-state pursuit[63] 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

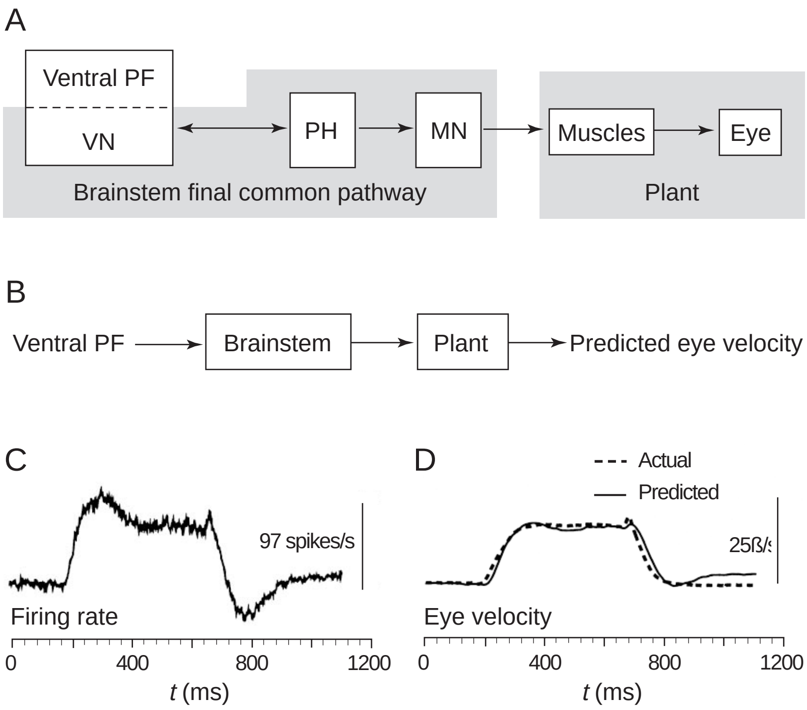

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Fig. 4. ***Eye-plant compensation provided by the cerebellum and brainstem during pursuit.*** **(A)** *The portion of the pathways for pursuit and saccades included in the simulation. The output from the ventral PF, conveyed by Purkinje cells, provides an input to brainstem nuclei that comprise the final common pathway for eye-movements. Motoneuron activity directly controls the eye plant.* **(B)** *A schematic diagram of the simulations used to test for plant compensation. Unit activity recorded in the ventral PF was provided as the input to a standard model of the brainstem pathways and the eye plant to produce a predicted eye-velocity output*[66]. **(C)** *The average differential firing rate used as the input for the simulations. This estimate of the bilateral input from both ventral PFs was obtained by subtracting the average of firing rate of 20 Purkinje cells during pursuit in the non-preferred direction from that during pursuit in the preferred direction.* **(D)** *Comparison of predicted (solid line) and actual (broken line) eye velocity. Abbreviations: MN, motor nuclei; PF, paraflocculus; PH, nucleus prepositus hypoglossi; VN, vestibular nuclei.* (C) and (D) reproduced, with permission, from Ref. 66.

PF during smooth eye-movements. These studies suggest that the brainstem–cerebellar pathways might be responsible for ensuring that the physical movement of the eyes matches the desired movement by appropriately compensating for the sluggish mechanics of the eye muscles and orbit (the oculomotor 'plant')[24]. The timecourse of the response of individual Purkinje-cell firing rates can be reconstructed by a weighted average of eye position, eye velocity and eye acceleration, suggesting that the output of the ventral PF could represent an 'inverse dynamics' signal[65]. In a more-direct test, when Purkinje-cell firing rate is used as the input to a model of the brainstem pathways and the eye plant, the output closely matches the observed timecourse of eye velocity (Fig. 4), demonstrating that the cerebellar signal indeed encodes an accurately plant-compensated eye-velocity command[66]. In contrast, the eye-movement inputs to the ventral PF are more sluggish and do not show compensation[62]. These observations can be viewed as a natural consequence of a control strategy that is based on object motion; if target motion has been determined upstream, then the only processing needed downstream for optimal control is plant compensation[43]. Furthermore, such a view is in agreement with the known involvement of the cerebellum in motor plasticity: as the eye plant changes throughout the lifetime of an individual, the neural circuits must adapt continuously in order to provide effective compensation. Whether these or other cerebellar regions also provide plant compensation during saccades has not been tested directly, although the cerebellum is clearly involved in adaptive changes of saccade metrics[67].

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 search the visual field for a unique target among a set of stimuli[68,69], and does so in direct relation to the difficulty in finding the target[28]. Similar increases in latency have been observed for pursuit when an observer must choose between two stimuli moving in opposite directions[70,71]. 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 similar but 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 fixated stimulus produces parallel decreases in the latency of saccades and pursuit to a second stimulus (the 'gap effect')[72]. 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 quantitatively 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[73].

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[74] or from *a posteriori* analysis of the sensory cue to target location[75]. Furthermore, at least some of the eye-movement-related neurons in the rostral SC are involved in the control of pursuit as well as saccades, suggesting that activity in this region could reflect target-location information available to both small saccades and pursuit[9]. Several cortical areas also appear to be influenced by or to participate in target selection. Saccade-related neurons in FEF and LIP respond more strongly when the stimulus in their response field is a target or behaviorally relevant than when it is a distractor or irrelevant[76–78]; unfortunately, similar tests have not been made of the pursuit-related responses in these areas[6,79,80]. Furthermore, the timecourse of saccade-related activity in FEF is appropriate for regulating the decision of when to initiate or cancel a saccade[81], and appears to be linked to salience-induced differences in perceptual reaction time during search[82]. Finally, in MT and MST, neurons exhibit stronger responses for pursuit targets or behaviorally relevant motion stimuli[83–85].

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 vermis in monkeys[14]. 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 might influence the decision to correct ongoing tracking errors with either a saccade or a smooth change in pursuit velocity. In addition, the transition point between the two types of eye movement depended on whether the monkey was fixating or pursuing, and on the direction of pursuit. This dependence suggests that the threshold for deciding whether to make a pursuit or a saccadic eye-movement depends on the current motor state. The putative role of 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[9–11] 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.

Déjà 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 subsystems became so firmly established. Nearly 40 years ago, Rashbass clearly established a fundamental link between the control of saccades and pursuit by showing that saccades can even be aborted if future pursuit alone is projected to track the target accurately[86]. Shortly afterwards, Young and colleagues[87] proposed a linked saccade and pursuit model in which tracking eye-movements were driven by target motion in the world. Steinbach[40], and Kowler and Steinman[88], argued early on that perception and cognition had major influences on eye movements. This article has outlined a more-explicit version of this viewpoint by relating it to a subset of the intervening 20 years of physiological, perceptual and behavioral studies. Although lower-order visual processes can drive reflex-like motor responses independently of perception (for example, the earliest component of the vergence response to disparity[89]), the examination of pursuit and saccades in more-complex scenarios provides a new opportunity for deciphering the mechanisms of higher-order vision.

The issues raised in this article also touch on a fundamental neurobiological question: what is the relationship between perception and voluntary motor action? As an extension of the distinction between the ventral 'what' and dorsal 'where' cortical streams of visual processing[90], it has been proposed that the cortical pathways for perception and action coincide with these ventral and dorsal streams, respectively[91]. Contrary to this view, the findings reviewed here concerning areas MT and MST clearly demonstrate that the 'where' information processed by these dorsal areas guides both perception and voluntary eye-movements. Whether or not the 'what' information processed within the ventral stream also affects voluntary eye movements remains unresolved. The preliminary finding, that changes in object shape can cause parallel changes in both motion perception and pursuit (even when object and local image motions are kept constant), suggests that 'what' information could indeed affect eye movements as well as motion perception[92], but resolution of this question requires further study.

In conclusion, rather than being controlled by two separate systems that transmit features of the retinal image to separate output motor pathways, this article proposes that pursuit and saccadic eye-movements are accomplished jointly by a cascade of processes that analyze and segment the retinal image, perceptually 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.

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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, neurones, 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.

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OVER 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, heartbeat, locomotion and vocalization). Insights into how organisms maintain their internal environment so that they are able to plan, and stay fit to execute, behavior are equally important for our understanding. Research over the past few years has shown that both afferent and efferent neurones, which are termed 'sensing effectors', process information and take appropriate action: for example, monitor and adjust blood-sugar levels, external osmolality 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 cells, for example, to the endocrine cells that regulate Ca^{2+} or sugar levels in mammalian blood.

Although integrated into the neuroendocrine system, sensing effectors bypass its rigid hierarchy by having their own 'smart' sensors to detect, and the secretory machinery to adjust, a specific metabolic parameter. If necessary, they will take commands from higher centres and can receive additional input. Sensing effectors that are involved in housekeeping resemble proprioceptors, which provide information from the internal

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