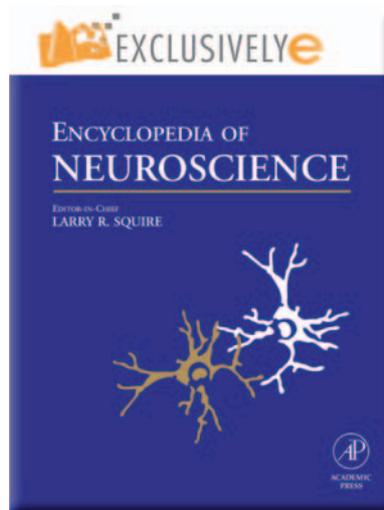


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Perception and Eye Movements

L S Stone and B R Beutter, NASA Ames Research Center, Moffett Field, CA, USA

M P Eckstein, University of California at Santa Barbara, Santa Barbara, CA, USA

D B Liston, San Jose State University Foundation, NASA Ames Research Center, Moffett Field, CA, USA

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The study of eye movements has long enjoyed a special status in biomedical research. First, compared to other sensorimotor systems, quantitative visual stimuli are relatively easy to create and quantitative eye movement measurements are relatively easy to acquire. Second, prior to the development of advanced imaging technologies, eye movements were the most important noninvasive diagnostic tool to localize brain pathology. Third, the eyeball has a constant rotational inertia and does not lift anything; thus, eye movements can be made largely independent of the on-line proprioceptive feedback needed to calibrate the force-displacement relationships of other motor systems. In summary, oculomotor control was perceived to be a straightforward, simple model system for understanding human sensorimotor control.

On the motor side, the 1960s brought about a revolution in oculomotor research, driven largely by the work of David A Robinson and Robert Wurtz. These researchers pioneered the combined use of the rigorous analytical tools of linear systems theory and of the powerful new experimental capability to reliably and precisely monitor eye movements while recording for extended periods of time from single visuomotor neurons of monkeys performing oculomotor tasks. In the subsequent half century, by systematically tracing, recording from, lesioning, stimulating, and ultimately modeling the major oculomotor pathways in cortical and subcortical structures, their two laboratories and those of their scientific progeny and colleagues made amazing progress in extending our understanding of how visual signals are transformed into eye movement motor commands.

On the vision side, the 1960s brought a similar revolution with John Robson, Fergus Campbell, Christina Enroth-Cugell, and others applying linear systems theory to visual perceptual performance. The 1980s brought a second revolution in vision science driven by David Marr and others, who applied a machine vision, computational perspective to human vision. Their synthetic approach of seeking biologically inspired (and constrained) solutions to real-world engineering and robotics problems by emulating the information processing within the human brain served to

highlight the full complexity of the visual processing needed for the effective control of motor actions.

During approximately the past two decades, it has become increasingly clear that the initial hope of the 1960s – that quasi-linear feedback models that transform a retinal position signal (and its derivatives) into an eye position signal (and its derivatives) might explain the critical aspects of voluntary oculomotor behavior – was overly optimistic. Indeed, recent results have highlighted that highly complex and non-linear aspects of visual perception play a critical role in guiding both voluntary smooth pursuit and saccades. Decades of research using small-spot visual stimuli that were nearly infinitely detectable, identifiable, and localizable revealed much about the motor factors and circuits that limit human oculomotor performance; however, much less was learned about the visual mechanisms that both limit and enrich oculomotor performance. A number of laboratories have begun to measure human saccadic and pursuit performance under more realistic visual conditions in order to examine how visual processing shapes oculomotor behavior.

Action and Perception

In 1982, Ungerleider and Mishkin made a major contribution to our understanding of primate visual information processing by identifying two major ascending processing streams through extrastriate cortex: a dorsal stream through parietal cortex with a hierarchical set of areas that focus on static and dynamic spatial characteristics of the stimulus (the ‘where’ pathway) and a ventral stream through the inferotemporal cortex with a hierarchy of areas that focus on identifying features of the stimulus (the ‘what’ pathway). Later, based largely on clinical observations, Goodale and Milner pushed this dichotomy a step further by proposing that the dorsal and ventral streams represent separate, largely independent, visual pathways supporting action and perception, respectively. They argued that object shape information from the ventral stream used for perception is not available to motor systems, and that spatial information from the dorsal pathway was not available to support perception. The critical finding from Newsome’s laboratory that local microstimulation of the middle temporal (MT) or medial superior temporal (MST) areas generates spatially localized and directionally specific biases in visual motion discrimination performance demonstrates that the dorsal pathway does play a major causal role in perception. However, these

findings do not rule out the possibility that ventral stream information may be inaccessible to motor systems.

A careful reexamination of early reports of dissociations of visual responses for perception and action used to support the Goodale–Milner hypothesis has shown that the purported failure to find a vulnerability to visual illusions for motor actions could be accounted for by subtle differences in the visual demands of the perceptual and motor tasks or by offsetting effects of a misperceived target location and of a distorted motor reference frame that obscure the visual impact of the illusion on motor action. When perception and motor actions are tested either simultaneously or using carefully matched conditions and

tasks, both are similarly vulnerable to illusions and other properties of the visual stimulus, undermining the view that visual information for perception is not shared with those systems controlling motor actions.

This article reviews key findings in the recent literature examining the extent to which the visual signals supporting perception are also used to drive voluntary human smooth pursuit and saccadic eye movements.

Smooth Pursuit and Visual Motion Perception

The linear systems view of pursuit has been dominated by retinal image motion models (Figure 1(a)). In this view, pursuit is essentially a simple, quasi-linear,

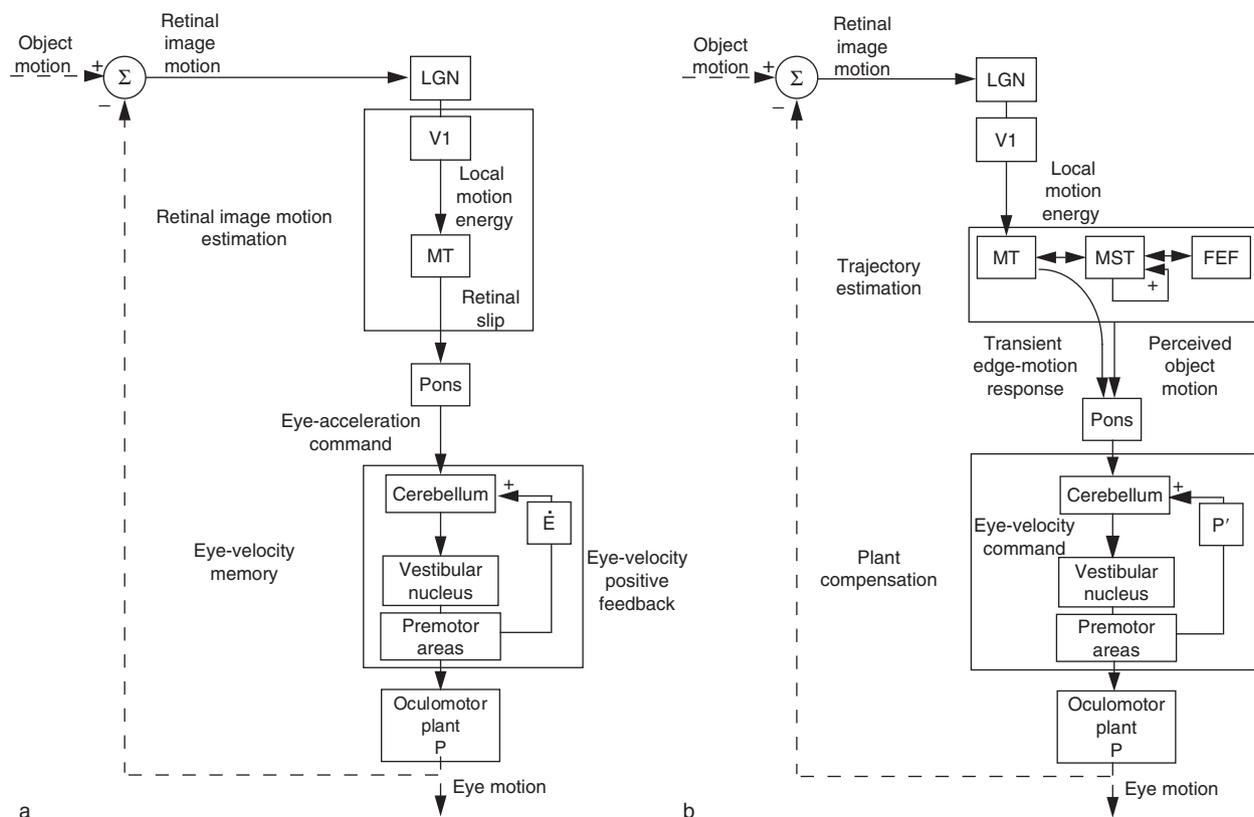


Figure 1 Pursuit models. (a) Retinal image motion models. In this framework, retinal image motion is analyzed in area MT (and associated extrastriate cortical areas in the superior temporal sulcus) to generate retinal position, velocity, and acceleration error signals. Weighted versions of these signals are summed and then sent to the brain stem–cerebellar structures as a command for pursuit eye acceleration. A positive feedback loop between the brain stem and cerebellum sustains ongoing eye velocity and integrates the eye-acceleration commands to generate changes in eye velocity. (b) Object motion models. In this framework, retinal image motion is first segmented in order to identify local edge motions which are subsequently selectively integrated to yield a measure of object motion. To attempt to resolve the inherent ambiguities in this problem, bottom-up retinal motion data, top-down cognitive assumptions and expectations, and either feed-forward or feedback signals related to ongoing eye motion are combined in a sluggish process that involves at least parietal and frontal cortex. The resulting visual object–motion signal is then sent to brain stem–cerebellar premotor circuits that prefilter the object-motion signal to compensate for the oculomotor plant before sending it on to motor neurons as the command for eye motion. (a) Adapted from Lisberger SG, Morris EJ, and Tychsen L (1987) Visual motion processing and sensory–motor integration for smooth pursuit eye movements. *Annual Review of Neuroscience* 10: 97–129. (b) Adapted from Stone LS, Beutter BR, and Lorenceau J (2000) Visual motion: Integration for perception and pursuit. *Perception* 29: 771–787.

continuous control system that attempts to minimize retinal image velocity through negative feedback. A retinal motion error signal or retinal slip (primarily a retinal velocity signal) is computed in area MT and sent to the brain stem as a command to drive eye acceleration. Meanwhile, ongoing eye velocity is maintained by a positive feedback circuit through the cerebellum which acts as an integrator of the acceleration commands. Although retinal image motion models can do a good job of explaining pursuit responses to a single white spot moving on a dark background (the only situation in which retinal image motion is identical to object motion), they cannot explain human pursuit responses to the wider range of visual conditions (and retinal stimuli) experienced when tracking a realistic object (which generates a set of disparate retinal local-edge motions) across a realistically textured environment.

Early studies revealed problems with the core idea that retinal motion error and eye velocity positive feedback form the command signal ultimately driving pursuit eye movements. The earliest pursuit studies observed zero phase-lag pursuit of sinusoidal motion, demonstrating a predictive component to the pursuit response that cannot be accounted for by eye velocity memory. In 1976, Steinbach showed that humans could pursue the horizontal motion of a rolling wagon wheel when only a few illuminated dots were visible on the rim. The perceived horizontal motion of an invisible rolling wheel is tracked, even though the retinal motions of the visible dots are cycloidal. Any observer who pursues this wagon wheel stimulus becomes immediately aware that pursuit does not simply respond to the motion in the retinal image. An additional red flag was raised in 1988 when Newsome, Wurtz, and Komatsu found signals related to ongoing eye motion in area MST, an area shown by both lesions and microstimulation studies to be causally involved in motion perception as well as generating the motor command for pursuit. Thus, the cortical signal driving smooth pursuit is not simply a retinal error signal but, rather, one more related to object motion in head- or world-centric coordinates. Moreover, that same year, Dursteler and Wurtz found that MST lesions cause direction-specific pursuit deficits, with no effort to make smooth corrections of the large residual retinal motion error during the poor steady-state tracking performance. These findings put into question any model of pursuit that proposes a negative feedback circuit that simply attempts to drive retinal motion to zero.

Numerous studies have shown clear links between pursuit and perceived motion, further distancing pursuit behavior from raw retinal velocity errors. First, perception and pursuit show the same speed and

direction discrimination performance and are similarly affected by nonlinear directional anisotropies such as the oblique effect, suggesting that rate-limiting neural speed and direction signals are shared by perception and pursuit. Furthermore, analysis of the trial-by-trial variation in human perceptual and pursuit direction responses shows higher correlation than expected by chance from independent mechanisms (Figure 2(a)). Thus, perception and pursuit share a limiting internal direction noise source, thereby undermining the theory that pursuit and perception have separate and independent, but fortuitously equal, underlying direction signals. Second, high-level cognitive expectations affect perception and pursuit equally. For example, in 2001, Krauzlis and Adler showed that when the likely direction of stimulus motion is cued prior to each trial, humans generate similar perceptual and pursuit performance biases toward the likely direction. Third, pursuit and perception appear to be fooled in the same way by visual illusions. For example, in 1996, Ringach, Hawken, and Shapley showed that humans generate a pursuit vergence response to the illusory motion in-depth of the kinetic depth effect. Fourth, the time course of the computation of object motion is similar for perception and pursuit. In particular, a human psychophysical study by Shiffrar and Lorenceau in 1996 and a human pursuit study by Masson and Stone in 2002 showed that the temporal integration of an initial set of local edge motion signals into a bona fide object motion signal is similarly sluggish (on the order of a few hundred milliseconds) for both perception and pursuit. In 2001, Pack and Born found a similarly sluggish temporal evolution of the direction signals encoded in the firing rate of MT neurons and those driving smooth eye movements in monkeys. Fifth, when presented with ambiguous image motion, perception and pursuit choose the same arbitrary interpretation of object motion, influenced by the same static image properties. In particular, when Madelain and Krauzlis asked observers to pursue a motion stimulus whose direction is completely ambiguous such that an observer can select a leftward or rightward percept at will, each perceptual reversal was associated with a pursuit reversal. Furthermore, on average, the perceptual reversal precedes the pursuit reversal by nearly 100 ms, consistent with perception driving pursuit within an object-motion pursuit model (Figure 3).

Finally, in 2001, Alais and Lorenceau showed that the spatial configuration or shape of ambiguous line drawings affects their perceived motion. In this regard, humans show similar effects of object shape on pursuit (Figure 4). For example, the motion of a diamond occluded by vertical windows appears rigid and is both veridically perceived and accurately

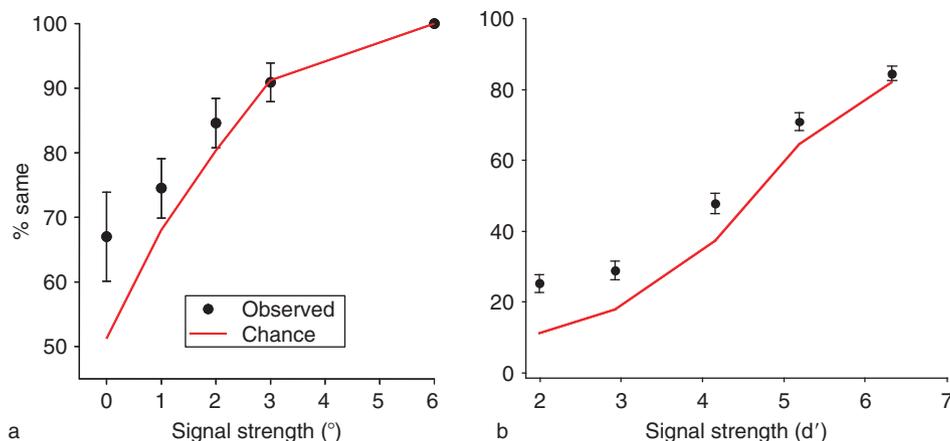


Figure 2 Covariation analysis (also called % same or choice probability). (a) Shared internal direction noise for pursuit and perception. In a simultaneous study of perceptual and pursuit direction signals, the binary psychometric and oculometric decisions were highly correlated across the entire range of signal strengths tested. The correlation expected by chance for two independent mechanisms is 50% in the no-signal condition and increases monotonically to 100% in the high-signal condition in which both decisions are always correct and therefore trivially the same. This figure plots the % same (the percentage of trials for which the pursuit and perceptual binary direction decisions were the same) for a single observer as a function of signal strength (direction difference in degrees from a cardinal axis). Note that the observed correlation was significantly higher than expected by chance (error bars show 95% confidence intervals). (b) Shared response to external noise for saccades and perception. In sequential studies of perceptual and saccadic localization with an identical set of noisy search images, the 10-alternative forced choice (10AFC) psychometric and oculometric decisions were correlated across the entire range of signal strengths tested (signal-to-noise levels in d' units). The correlation expected by chance from two independent mechanisms is 10% in the zero SNR condition and increases monotonically to 100% for an extrapolated high SNR condition in which both decisions are always correct and therefore trivially the same. This figure plots the % same (the percentage of image samples for which the perceptual and saccadic 10AFC decisions were the same) for a single observer as a function of signal strength (ratio of peak luminance of the target to the amplitude of the pixel luminance noise). Note that the observed correlation was significantly higher than expected by chance (error bars show standard errors). (a) Adapted from Stone LS and Krauzlis RJ (2003) shared motion signals for human perceptual decisions and oculomotor actions. *Journal of Vision* 3: 725–736. (b) Figure based on data from Beutter BR, Eckstein MP, and Stone LS (2003) Saccadic and perceptual performance in visual search tasks: I. Contrast detection and discrimination. *Journal of the Optical Society of America A* 20: 1341–1355.

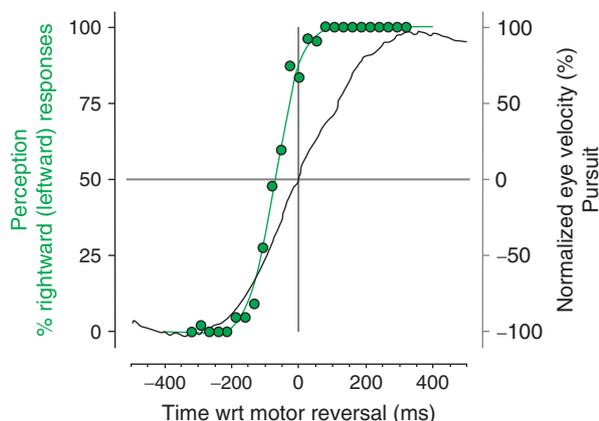


Figure 3 Correlated pursued and perceived direction reversals for completely ambiguous motion. For a stimulus that can be perceived as moving rightward or leftward at will, the data show that the perceptual reversal (plotted as percentage rightward or leftward judgments) preceded the oculomotor direction reversal (plotted as mean eye velocity) by slightly less than 100 ms, consistent with perceived motion driving pursuit. The retinal image motion is constant throughout but pursuit changes from rightward to leftward (or vice versa) synergistically with the reversals in perceived motion, which is inconsistent with all retinal image motion models of pursuit. Adapted from Madelain L and Krauzlis RJ (2003) Pursuit of the ineffable: Perceptual and motor reversals during the tracking of apparent motion. *Journal of Vision* 3: 642–653.

pursued. However, the motion of a similarly occluded cross (defined by the exact same segment image motion but merely spatially rearranged) is perceived as non-rigid; the coherent two-dimensional (2-D) object motion interpretation is presumably interfered with by the distracting vertical motion of the segments. Pursuit of a diamond moving along an isotropic trajectory shows an isotropic response (i.e., vertical and horizontal pursuit gains are equal), consistent with the motion of a rigid object. However, pursuit of the cross shows lower overall gain and a clear vertical bias, consistent with the nonrigid object motion percept and the vertical segment motion inference. This finding suggests that object shape information, presumably from the ventral pathway, is influencing perception and pursuit in parallel. Moreover, even an extended version of the retinal image motion model that attempts to minimize the sum (or vector average) of all the retinal segment motions would predict that pursuit of the cross and pursuit of the diamond would be identical.

The emerging picture is that pursuit is driven by a signal related to perceived object motion and not directly by retinal image motion. An object motion model of pursuit (Figure 1(b)) can not only explain

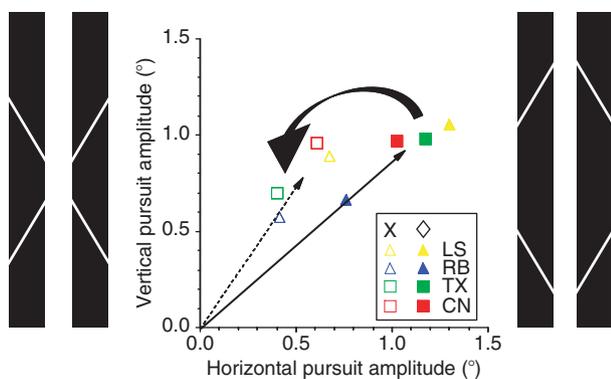


Figure 4 Different pursuit for identical retinal motion related to differences in object shape. Moving occluded line figures with identical object motion trajectories and identical segment motions (but with the segments in different relative retinal locations) can nonetheless be perceived and pursued differently. The data show the horizontal and vertical pursuit amplitudes of four observers in response to a diamond (solid) or a cross (open) configuration representing the same object motion along an isotropic 2-D Lissajous figure. The diamond is perceived to move rigidly and is pursued with an isotropic high-gain response. The cross, however, appears to move nonrigidly and is pursued with a low-gain trajectory biased in the vertical direction of the segment motion. The fact that both of these stimuli generate 2-D trajectories at all is inconsistent with retinal image motion models, which would generate nearly exclusively vertical pursuit in response to the vertical retinal segment motion. More important, the fact that identical physical object motion is pursued differently when different non-motion information generates different object motion percepts is strong evidence that pursuit is driven by an object motion signal shared with perception. Adapted from Stone LS, Beutter BR, and Lorenceau J (2000) Visual motion: Integration for perception and pursuit. *Perception* 29: 771–787.

the wider range of new phenomena described previously but also takes into consideration the wealth of physiological findings demonstrating an extensive role for both parietal (MST) and frontal (frontal eye field (FEF) pursuit area) cortex in trajectory estimation (including prediction). It also acknowledges that these areas, not just MT, provide a major component of the descending pathway to brain stem and cerebellar structures involved in the generation of the motor output signal driving pursuit. The role of cortex in this new view is not to calculate derivatives of retinal motion but, rather, to compute a best estimate of object motion from the available visual information (both dynamic and static) within a cognitive and attentional context. If an object motion signal is sent down to the brain stem (instead of a retinal error signal), then the role of the cerebellar feedback loop must also be reassessed. If object motion is the descending cortical output signal, then the only processing needed to optimize the oculomotor command to the plant is to high-pass prefilter the eye velocity command to compensate for the low-pass filtering of the oculomotor plant. Indeed, the output signals

from the cerebellum supporting pursuit have been shown to be a prefiltered version of the subsequent eye velocity signal. Such prefiltering could be achieved via a positive feedback loop that mimics the plant. Another important virtue of this model, in addition to its ability to reconcile a wide range of behavioral and physiological pursuit observations, is that it is easily generalized to other motor systems, whereby the cerebellum would act as a compensator for other motor plants all driven by the same cortical object motion signal (or another relevant perceptual signal). Thus, the hand and the eye can work synergistically when tracking a moving object.

Saccades and Visual Target Selection

The linear systems theory view of the saccadic system has been dominated by variants of a retinal offset model (Figure 5(a)). In this view, the saccadic system is essentially a simple, quasi-linear, bang-bang control system that rapidly corrects retinal position offset by driving this offset to zero through negative feedback. A retinal position error signal from primary visual cortex (V1), modulated by inputs from other cortical areas, is sent down to the superior colliculus (SC) of the midbrain as the retinal target position signal. When a particular locus in the SC map reaches a threshold, that location relays a command for desired eye position to brain stem structures that generate the neural pulse and step signals needed to accelerate the eye and then hold it in its new position, respectively. Although this model includes a detailed description of brain stem structures, as with the retinal image motion pursuit model, the entire visual and decision-making process is the trivial calculation of an unambiguous retinal error signal – in this case, position instead of velocity. Again, such a retinal signal is only unambiguous in the degenerate case of a small spot on a dark background. Furthermore, it has long been known that nonretinal signals can drive voluntary saccades, such as auditory or visual memory signals.

During approximately the past decade, a number of laboratories have turned their attention to understanding the visual processes underlying saccadic target selection in search and search-like tasks using more realistic visual stimuli with targets of variable signal strength, embedded in external image noise, among similarly salient nontarget ‘distractors,’ and/or with differing *a priori* location probabilities. These studies have revealed a rich complexity of signal processing, requiring broadly distributed interactions between parietal and frontal cortex and the midbrain.

Numerous studies have illustrated clear links between saccades and perception, further distancing saccadic behavior from raw retinal offset signals. First, it

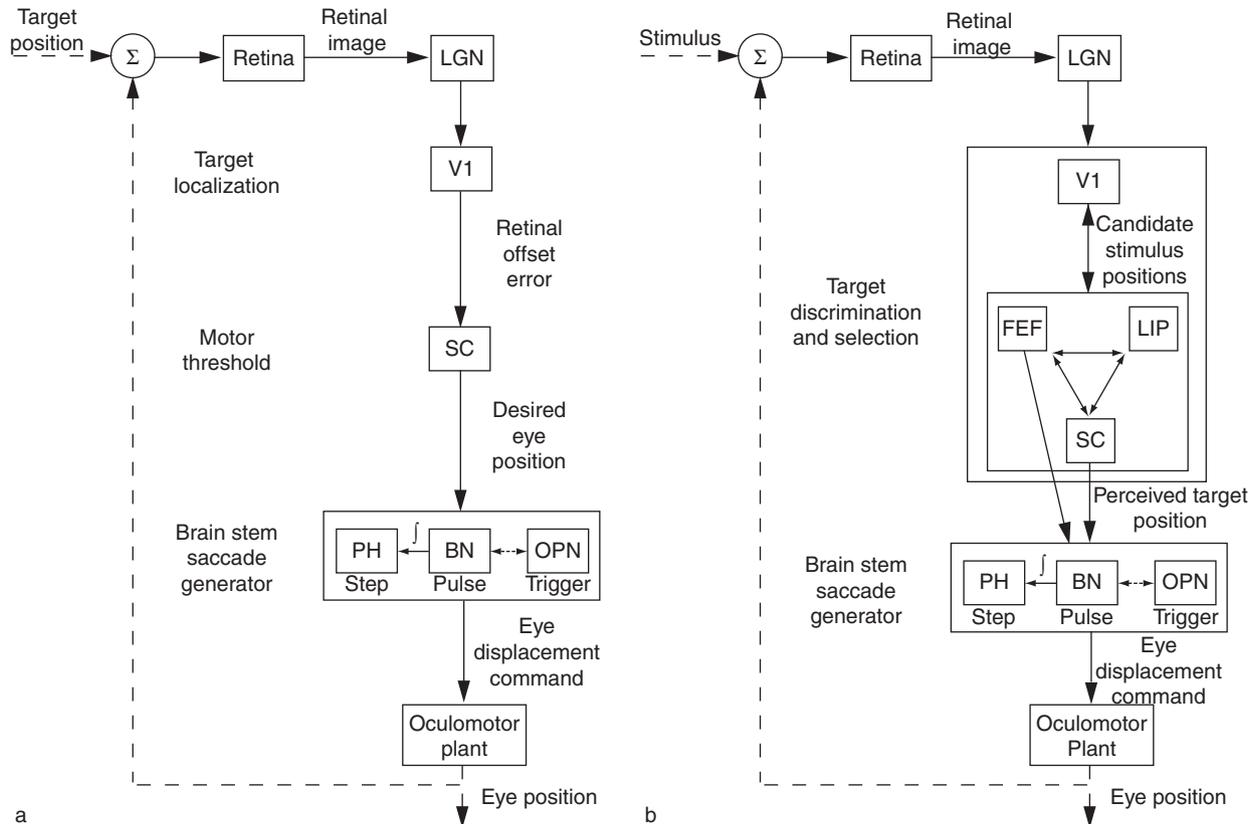


Figure 5 Saccade models. (a) Retinal offset error models. In this framework, a retinal offset signal is computed in primary visual cortex (V1) (with input from parietal and frontal cortical areas) and then send to the superior colliculus (SC) of the midbrain. When that signal reaches threshold, the SC sends a desired eye position signal to brain stem saccadic structures, which generate the command for eye displacement. (b) Target selection models. In this framework, the totality of the retinal image is processed in parallel to identify candidate target locations. A network that includes the lateral-intraparietal area (LIP), the frontal eye fields (FEF), and the SC works to select a single target using the available bottom-up sensory data modulated by top-down cognitive and attentional factors. The resulting perceived target position signal is then sent to brain stem saccadic structures, which generate the command for eye displacement.

has been shown that saccades and perception appear similarly affected by spatial illusions. For example, saccades (and hand pointing as well) show systematic spatial deviations in the same direction as the spatial misperceptions for stimuli that evoke the Muller-Lyer illusion. Although early reports of this effect on saccades were conflicting, when the saccadic task relies on a visual feature that is distorted by the illusion, the motor response reflects the perceptual illusion. Second, contrast detection and discrimination thresholds are equal for perception and saccades. More important, using noisy search stimuli, the correlation between the external image noise-driven responses of saccades and perception is higher than expected by chance from two independent mechanisms (Figure 2(b)). Thus, saccades and perception appear equally vulnerable to those random spatial features of a particular noise sample that appear target-like. Third, using classification image analysis (a form of reverse correlation), by combining the hundreds of noise samples (sans target) that generated erroneous responses, one can

construct an image of the virtual target that saccades and perception were looking for (i.e., an estimate of the template or overall receptive field used in the decision-making process). Not only are the shapes of the classification images from saccadic and perceptual decisions indistinguishable but also their common shape differs significantly from that of the target (Figure 6). Indeed, both images are a high-passed version of the target, which may indeed be optimal if one is searching for the target embedded in the low-pass filtered noise commonly associated with visual neural signals.

The emerging view is that a complicated network between the parietal and frontal cortex, as well as the SC, converges to select a single target using both bottom-up sensory data and top-down cognitive knowledge, expectation, and/or anticipation of reward. Furthermore, ascending feedback from the SC to visual cortical areas appears to play an important role in this process by driving attention-like modulations of visual processing, thereby influencing

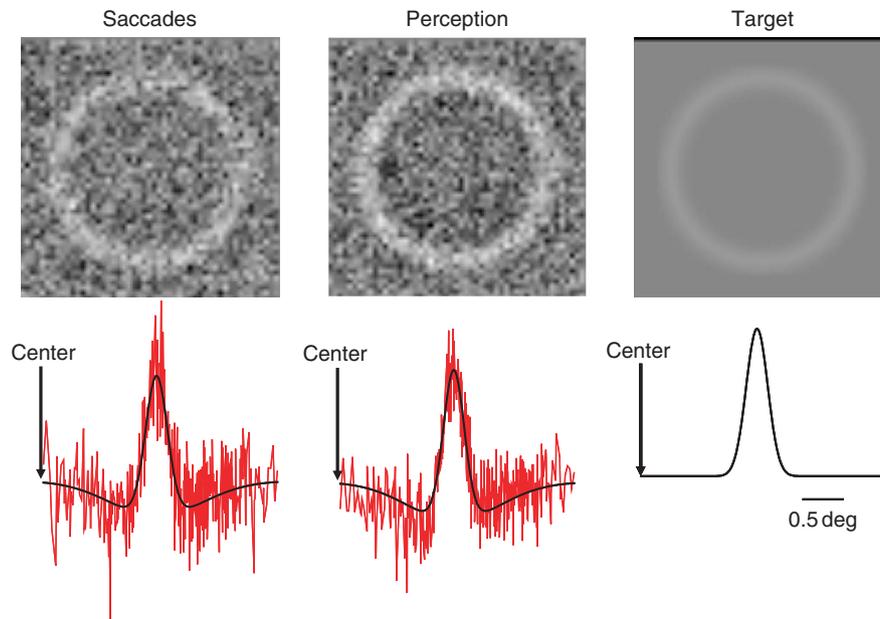


Figure 6 Classification image (CI) analysis reveals the saccadic and perceptual ‘receptive field’ used to search for the brightest ‘O’ among dimmer Os. The top row shows the raw CI for saccades and perception, respectively. The bottom row shows the normalized and polar averaged cross-section of the receptive fields. Note that the perceptual and saccades receptive fields are both high-pass filtered versions of the Gaussian stimulus cross-section and are well described by difference of Gaussian functions (solid black lines under the red data traces). Thus, not only is the receptive field shape the same for saccades and perception but also the perceptual and saccades receptive fields are more similar to each other than they are to the actual target, providing strong evidence of a shared target template used by perception and saccades during search.

perception, although the exact nature of these modulations is not well understood. The target selection model of saccades (Figure 5(b)) acknowledges the simple fact that the saccadic system is not finding a single target presented in a vacuum but, rather, is selecting the most behaviorally relevant target from among many candidate possibilities. Thus, rather than thinking of visual target localization as a trivial thresholding of a single highly salient spot, studies have reframed saccadic targeting within the context of signal detection theory, addressing the nontrivial question of how to decide where to look next when the target is inconspicuous or is similar to surrounding distractors. Saccadic and perceptual search can be described as a template-matching task in the presence of noise and spatial uncertainty; the template captures essential contrast and shape information about the searched-for target albeit not necessary perfectly matched to the target (Figure 6). Indeed, the similarity of the classification images for perception and saccades (and their shared difference with the actual target shape) strongly suggests that the saccadic system has access to the same shape information as perception, presumably from shared ventral pathways supporting both perception and action.

Although the new framework for saccadic targeting embraces a novel view of visual processing, unlike

pursuit, the proposed new visual front end for saccades does not require a fundamental reinterpretation of the role of brain stem saccade-generating structures. However, it is becoming increasingly clear that the SC is not merely a feed-forward output relay to brain stem structures but, rather, plays a key role in the target selection process, along with the lateral intraparietal (LIP) area and the FEF. Consistent with this distributed responsibility for target selection, Schiller and colleagues showed that bilateral removal of either the SC or the FEF leaves the ability to make saccades intact, whereas bilateral removal of both areas destroys that ability. Furthermore, studies in both the Wurtz and Newsome laboratories have demonstrated that stimulation of the SC can modulate perceptual performance, justifying the elevation of the SC into the target-selection network, which was formerly considered to be exclusively cortical.

A New Framework for the Visuomotor Control of Pursuit and Saccades

The major paradigm shift that has occurred in the study of pursuit and saccades is the realization that the visual processing part of the sensorimotor problem is more complicated than originally thought.

When humans 'see' by taking the neural signals coming from the approximately 1 million ganglion cells in each eye to create a full-color 3-D model of the world around them, quite a complicated process has occurred. The sensory information available represents two 2-D projections of the world, one from each retina, and is therefore necessarily incomplete. The human visual system must use the available sensory data (bottom-up information) as well as *a priori* knowledge about the world (top-down information) to infer a best guess of what is actually out there. As such, all visual perception is illusion; what we call illusions are merely those rare instances when the brain's best guess is obviously wrong.

Complex interactions between frontal, parietal, inferotemporal, and occipital cortex, along with the midbrain, are used to combine bottom-up and top-down information into a time-varying best estimate of the oculomotor target. For pursuit, the reconstruction of the target object's motion in the world takes time. An early quick estimate of object motion using the vector average of local edge motions appears to drive early perceptual and pursuit responses, with a more accurate estimate emerging with a time constant on the order of 100 ms. The standard linear system control theory approach of considering only the initial 100-ms 'open-loop' pursuit response to characterize the internal visuomotor transfer function therefore misses much of this elegant, yet sluggish, computational process. Object motion estimation of realistic targets takes time because, after the initial sensory transduction, the visual system must first segregate from the background those pieces of the retinal image that represent individual local motion features. The system must then selectively integrate those pieces that properly belong together into a whole object whose global motion can then be computed. This process is inherently ambiguous because the data set is incomplete (although over time the ambiguity of the object trajectory can resolve itself). Thus, the perceptual and pursuit systems must make visual choices. The preponderance of evidence gathered during approximately the past decade argues that perception and pursuit make the same choice using shared visual motion processing mechanisms broadly distributed across parietal and frontal cortex, with likely input from inferotemporal cortex as well.

For saccades, localizing the target object is also a complex, time-consuming visual process involving both parallel and serial components: parallel because all portions of the visual field are being processed simultaneously and serial because, at low target salience, a sequence of discrete fixation steps is traced as one searches for the target. Presumably, during each

fixation, a target-like template is being compared with incoming noisy sensory data in order to determine the 'best' next location to foveate, with multiple locations constantly competing for attention. The preponderance of evidence indicates that perception and saccades make the same choices using shared spatial visual processing mechanisms broadly distributed between parietal and frontal cortex, with inputs from the superior colliculus and inferotemporal cortex as well.

Another difference between the traditional oculomotor models (Figures 1(a) and 5(a)) and the new frameworks (Figures 1(b) and 5(b)) is the coordinate system of the visual signals driving motor actions. The traditional view of saccades and pursuit assumes that the controlled visual signals are in raw retinal coordinates: retinal position, velocity, or even acceleration error signals to be minimized by negative feedback. Not only do the aforementioned MST studies rule this out for pursuit but also a behavioral study of the direction signals driving perception during fixation and pursuit by Krukowski and colleagues in 2003 showed that the limiting direction noise and even the oblique effect are not in retinal coordinates but, rather, in head- or world-centered coordinates. This finding shows that performance in an apparently simple direction discrimination task is limited by neural signals beyond area MT (the highest area mapped in retinal coordinates) and thus in area MST (an area in which retinal motion signals are combined with eye and head motion signals) or another motion area further along in the dorsal pathway. Indeed, there is even direct physiological evidence that some MST neurons encode object motion in world coordinates.

The cortical signals driving saccades are also not simply in retinal coordinates. LIP and FEF both encode target location in 'oculocentric' coordinates, which comprise a coordinate system in which target location is constantly being updated with respect to the current eye position using anticipatory signals about future eye movements (even in the absence of visual feedback). This updating process, first described by Colby, Duhamel, and Goldberg, effectively keeps the target location stably encoded in head-centered space – yet bouncing around in the retinal map with every saccade – presumably as part of the mechanism keeping the world perceptually stable during saccades. Sommer and Wurtz characterized an oculomotor feedback pathway from SC to FEF, via the mediodorsal thalamus, and have further shown that interruption of the corollary discharge signal from the SC disrupts the proper updating of target location, thereby demonstrating that the SC plays a key role in the coordinate system transformation for target localization performed within the cortex.

Clearly, the frameworks in [Figures 1\(b\) and 5\(b\)](#) are mere cartoons that require much fleshing out. Nonetheless, they succinctly represent the concatenation of a number of conceptual advances that are guiding the next generation of oculomotor researchers and cortical physiologists. Regrettably, this short article can mention only a small number of the many important recent findings. Many researchers are actively working to understand the visual processing for saccade target selection and pursuit object motion estimation and the associated neurophysiological underpinnings. Although much progress has been made, the picture of how an extended network of cortical (and even subcortical) areas interact to shape synergistic perception and sensorimotor control remains incomplete.

Conclusion

Because the sensory ‘image’ of the world is inherently ambiguous, humans must generate a best-estimate solution to this complex puzzle, using noisy incomplete data and cognitive strategies to construct an internal 3-D model of visual space, in order to interact with their environment and ultimately to survive in the real world. Perhaps, our coherent multisensory perception of the world evolved from the need for the brain to provide a single, decisive interpretation of an ambiguous and incomplete set of visual (and other) signals in order to coordinate the actions of multiple motor systems. Indeed, above and beyond the parsimony argument about limited cortical processing resources, it is difficult to imagine an evolutionary advantage of each neural system developing a set of independent, potentially conflicting, private solutions to the visual problems of detection, discrimination, and target selection.

See also: Active Perception; Attention and Eye Movements; Basal Ganglia and Oculomotor Control; Brainstem Control of Eye Movements; Cerebellum and Oculomotor Control; Contextual Interactions in Visual Perception; Cortical Control of Eye Movements; Eye and Head Movements; Eye Movement Disorders; Oculomotor Control: Anatomical Pathways; Optokinetic Eye Movements; Pursuit Eye Movements; Saccade–Pursuit Interactions; Saccades and Visual Search; Saccadic Eye Movements; Target Selection for Pursuit and Saccades; Vision for Action and Perception.

Further Reading

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