

Computation and physiology of sensory-motor processing in eye movements

Leslie C Osborne

Performance in sensory-motor behaviors guides our understanding of many of the key computational functions of the brain: the representation of sensory information, the translation of sensory signals to commands for movement, and the production of behavior. Eye movement behaviors have become a valuable testing ground for theories of neural computation because the neural circuitry has been well characterized and the mechanical control of the eye is comparatively simple. Here I review recent studies of eye movement behaviors that provide insight into sensory-motor computation at the single neuron and systems levels. They show that errors in sensory estimation dominate eye movement variability and that the motor system functions to reduce the behavioral impact of its own intrinsic noise sources.

Address

Department of Neurobiology, University of Chicago, 947 E 58th Street MC0928, Chicago, IL 60637, USA

Corresponding author: Osborne, Leslie C (osborne@uchicago.edu)

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Introduction

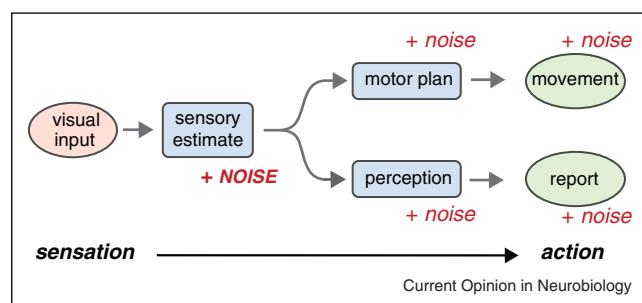
In the absence of a predictable world, our actions can only be informed through our senses. We cannot position a racket more precisely than we can see a ball, or aim a swatter more accurately than we can locate a fly. When behavioral performance is at a premium, the brain may seek to minimize internal noise and maximize information transfer from sensory areas that represent the event to motor areas that will generate the response. Computational strategies that might enhance behavioral performance include (1) increasing the amount of information encoded about a salient sensory event, (2) minimizing noise in sensory-motor processing, and (3) enhancing the precision of movement execution by optimizing motor commands and learning. The oculomotor system has several features that aid in the analysis of sensory-motor processing: the eye is controlled by three pairs of muscles, which simplifies modeling, the motor circuits that control the eyes are well understood, and eye

movement behaviors demonstrate all three areas of performance enhancement. In the past several years, remarkable progress has been made toward understanding visual and motor processing from a computational perspective. This review has two aims. The first is to articulate our current understanding of computation in sensory-motor processing in eye movement behavior with an emphasis on noise propagation. The second aim is to highlight the contribution that the study of eye movements has made to our general understanding of neural computation.

The information bottleneck in sensory-motor processing

Information in sensory-motor pathways, and ultimately the fidelity of behavior, is limited by noise that accrues at each stage of neural processing and of movement execution. In the oculomotor system, information about the location, direction, and speed of a visual target is translated into motor commands to move the eye and hold the target in sight. The fidelity of an eye movement will depend on how well the targeting parameters are estimated from visual signals, how efficiently sensory goals are translated into movement commands, and how precisely those commands are executed by the motor system. In humans and nonhuman primates, the initiation of smooth eye movements such as pursuit and the entirety of saccades are performed ‘open-loop’, driven solely by feed-forward image motion signals that originate in the retina [1,2]. These behaviors cannot be more precise than the visual representation of the target (in the absence of prediction) but can be less precise if noise accumulates downstream in the planning and execution of the movement. A growing number of studies support the hypothesis that variability in sensory estimation dominates movement variability. In this section, I highlight some of these recent results that suggest that sensory estimation, rather than movement production, is the information bottleneck in the oculomotor system.

To distinguish sensory from motor noise contributions to eye movement variability, several studies have compared the precision of eye movements and visual perception. Visual information about the target likely gives rise to both eye movement and visual perception because the pathway from the retina to visual cortex is shared between the perceptual and motor systems. However, common input pathways do not necessarily imply matched sensory estimates. For example, if activity in the visual system is decoded independently by the perceptual and motor systems, or if the two pathways are dominated by independent

Figure 1

A schematic of information flow from sensory to perceptual and motor areas. If noise in forming a sensory estimate is larger than the private noise sources in the perceptual and motor processing, then variability in behavior should be comparable to variability in perceptual reports.

noise sources, then mismatches between perception and motor commands may arise which in turn would lead to differences between eye movements and perceptual reports from trial to trial (Figure 1).

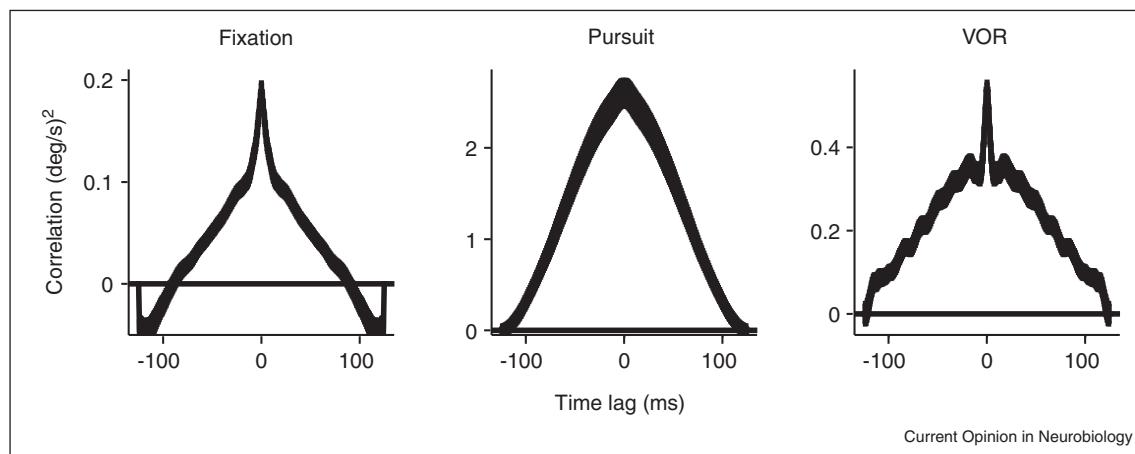
Schutz *et al.* [3•] tested the hypothesis that sensory input, and thus sensory noise, is common to both perception and eye movements, by testing pursuit and perception of various types of random dot kinetograms. They report that pursuit eye speed and perceived target speed are quite similar across several types of motion stimuli, and that both are identically affected by motion coherence levels. They conclude that ‘the same neural machinery’ drives both pursuit and perception. These results agree with earlier work that found that oculomotor thresholds increase along with perceptual thresholds for targets with added directional and speed variation [4,5], and that errors in pursuit and motion perception are correlated from trial to trial [6; but see also 7,8].

The finding that sensory noise dominates eye movement variation is not unique to smooth pursuit. Two recent studies draw similar conclusions about saccades and the vestibular ocular reflex (VOR), which share motor effectors but have different sensory inputs than smooth eye movements. To examine the contributions of sensory noise in target localization for saccades versus motor noise in the command and execution in the movements, van Beers [9] constructed a detailed computational model with both sensory and motor noise components to compare to measured saccadic endpoint variability. Acuity in the localization of visual targets is not uniform across the visual field, but varies systematically with distance from the fovea and direction. Van Beers found that variability in saccade endpoints scaled with the changing precision in visual localization and that sensory noise accounted for nearly three times more of the variance than did motor noise. Using a different modeling approach (described in the next section), Munuera *et al.* obtained a similar result [10].

If eye movement variation arises primarily in the visual system, an oculomotor behavior driven by nonvisual input should have substantially different levels of variation from visually driven behavior. Guo and Raymond [11] compared the variation in smooth eye velocity arising from visual motion to vestibularly driven eye movements in the dark (see also [12]). When a monkey relied on visual input to drive eye movements, as during smooth pursuit, eye velocity was more variable than when vestibular input alone drove the eye movement. Figure 2 compares the temporal structure and scale of eye velocity variation in fixation, and for speed matched, open-loop VOR and smooth pursuit responses. Fluctuations in eye velocity from three different behaviors covary over different time scales, from <10 ms for fixation to >50 ms for smooth pursuit, and thus the effective number of dimensions needed to describe eye movement fluctuations differs for each behavior. If noise in motor neurons or in muscle contraction were dominant, we might expect variation in each of these behaviors to be comparable because the motor effectors are common across all three behaviors.

Fluctuations in neural responses within the oculomotor pathway should be more highly correlated with fluctuations in eye movements if the neurons are downstream from the dominant noise source than if upstream. Medina and Lisberger [13••] demonstrated that variation in pursuit is driven by noise sources that are at or upstream from the cerebellum. Isolating single Purkinje neurons in the floccular complex of the cerebellum that mediate pursuit, they correlated trial-to-trial fluctuations in spike count with fluctuations in eye velocity during pursuit initiation in highly trained monkeys. In order to express firing rate and behavior in the same units, they used the average neural and behavioral responses to fit a model of the relationship between firing rate and eye movement. They found that ~60–80% of the variation in pursuit initiation could be accounted for by variation in Purkinje cell firing rate, and that the correlation diminishes during the movement. This implies that variation in cerebellar activity during pursuit initiation is local, or is inherited from upstream cortical signals representing visual information about target motion, and that the dominant noise source moves downstream to motor areas as the control loop closes. Consistent with this finding, a study that measured correlations in eye velocity and perceptual judgments during sensory-driven pursuit initiation [6] found higher levels of correlations than a similar study of steady-state pursuit [7] which is controlled by a combination of retinal and extra-retinal signals [e.g. 14].

Is a sensory cortical origin for eye movement variability plausible? To determine whether variation in the visual motion estimates are sufficient to account for variation in pursuit, Huang and Lisberger [15•] examined the relationship between neural variability in the middle

Figure 2

The temporal structure of eye velocity fluctuations in fixation, and in the initiation of pursuit and vestibulo-ocular reflex (VOR) eye movements. Plots represent the auto-correlation of fluctuations in the horizontal component of eye velocity around the average movement (noise correlations). For pursuit and VOR, eye speed was well-matched throughout the movement. Error bars represent standard deviations. Pursuit and fixation data from [57]; VOR data courtesy Stephen Lisberger.

temporal cortical area (MT) and variation in eye velocity during smooth pursuit initiation. MT provides the visual inputs for both the perception of visual motion and for pursuit [16–24]. Using a vector-averaging model to decode target direction and speed estimates, they showed that both individual neural variation and the tuning of neuron–neuron correlations in the cortical population have a significant impact on pursuit variation. They concluded that neuronal variability in sensory cortex is of an appropriate scale to account for variation in pursuit initiation. While the simulation results are instructive, a more direct test of the connection between cortical population activity and eye movements awaits recording a larger sample of the sensory population encoding visual target motion during behavior.

Noise reduction in motor processing

The fact that sensory noise dominates movement variability suggests that the oculomotor system may use control strategies that minimize the consequences of motor-related variability. Hu *et al.* [25] find that pre-motor neurons in the pontine reticular formation fire repeatable patterns of inter-spike intervals, suggesting that precision is maintained by strong neuron–neuron correlations that serve to reduce noise in motor commands, a mechanism that may also minimize variability in the cerebellum [13**]. Muscle tension has intrinsic variation, including ‘signal-dependent’ noise that scales with force and therefore with the motor signal driving it [26**,27,28]. Two studies have suggested that the temporal structure of oculomotor commands for saccades could compensate for intrinsic noise in eye muscle contraction and thereby minimize the impact of execution noise on the variability of eye movements. Saccades are controlled by a stereotyped motor neuron

firing rate sequence, called the main sequence that creates stereotyped co-dependence of peak velocity, duration, and amplitude. Assigning cost to movement speed and accuracy, Harris and Wolpert [26**,29] showed that minimizing signal-dependent motor noise accounts for the velocity profile and duration of saccades. van Beers [30**] extended these ideas to include constant background and temporal noise sources and found that the more complete noise model could also account for the direction dependence of saccade velocity and its dependence on initial eye orientation. This suggests that saccades are generated with movement profiles that minimize the impact of all forms of motor noise.

Because eye muscles can fatigue, and movement commands must be based on the current tension of the eye muscles, the motor system must constantly update the command needed to produce the desired eye movement. The optimal way for the motor system to minimize the influence of noise on eye movements is to weight incoming signals according to their reliability [31]. Several studies have found evidence for optimal control in the oculomotor system. Munuera *et al.* [10] measured the relative contribution of motor command copy and visual feedback to the correction of subsequent saccades by introducing artificial errors with target jumps while the eye was in flight. They found that relatively little contribution is made by noise in motor neurons or muscles in agreement with studies described in the previous section. The success of an optimal control model to account for the experimental results suggests that humans use feedback signals optimally in saccades. Neural signals that would support such a computation have been found in the primate oculomotor system [32,33].

Utilizing the natural variation in reaching movements, which have larger errors than saccades, van Beers showed that the rate of motor learning, determined by how much errors correct the next movement command, is optimized to minimize endpoint variance [34^{••}]. He tested sequences of measured movement endpoint errors against a model of motor planning that included two sources of motor noise: movement execution noise (as in his saccade model mentioned above) and motor planning noise. In his model planning noise could represent variability in the generation of a signal representing the planned endpoint of the movement, or it might represent noise in an efferent copy of the motor command. Van Beers showed that about 38% of each error is corrected in the planning of the next movement, the learning rate for which movement endpoint variance is minimal.

Constraints on neural population coding of visual target features

To identify the origin of the limiting noise source in sensory-motor pathways and determine whether it is intrinsic to cortex or inherited from the sensory periphery, it will be necessary to trace the flow of stimulus information through the neural circuit. With the advent of extremely high-density recording, it has become possible to estimate the precision with which motion encoded by the retina. Frechette *et al.* [35[•]] estimate that retinal ganglion cell population activity encodes speed with a precision of approximately 1% for a high-contrast bar stimulus with constant drift. Perceptual and pursuit thresholds for speed discrimination are greater than 8% [23,36], suggesting that noise accumulates and information about motion speed is lost during subsequent visual processing. However, evidence for efficient coding has been observed in both peripheral and central visual areas. Information per spike increases across retinal-thalamic synapses [37[•],38[•]] and neurons in the visual system actively adjust their gain to maintain efficient coding of dynamic sensory stimuli [39–43,44[•],45[•],46^{••}]. If visual neurons are individually maximizing the information that they encode and transmit, they are unlikely to be intrinsically noisier than neurons in the motor system. Rather, the sensory errors that account for variation in perception and eye movements may arise in the decoding of the sensory cortical population.

Eye movement behavior can be more precise than individual sensory neurons.

Motion estimates for eye movements like pursuit arise in cortical area MT. Individually, the average MT neuron can discriminate motion direction to within 15–30° whereas pursuit and perceptual thresholds are 2–3° [36,47,48]. Speed discrimination thresholds for MT neurons average about 4 times larger than for perception [23]. To obtain high levels of behavioral and perceptual precision for eye movements, the brain likely derives

sensory estimates from activity across a population of neurons (e.g. [49–51]). The brain's mechanisms for decoding neural population activity are unknown and likely have a profound impact on the amount of stimulus information that brain can recover in order to guide behavior [52–54].

The speed, accuracy, and precision of eye movements place strong constraints on how visual information can be encoded in cortical populations and how that information is read out. For example, pursuit is initiated based on the first 100–150 ms of target motion. During this period, MT neurons fire three action potentials on average with a highly dynamic firing rate, especially when motion is near the preferred direction and speed [47]. For a decoding mechanism to maximize the information it recovers from this brief signal, it might be optimized to distinguish between short time scale events [55,56] such as patterns of spikes and silences across a neural population [53,54]. An ambition for future work is to connect eye movements to the decoding of sensory neuron populations in order to elucidate fundamental mechanisms of coding in the brain.

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