A physiological perspective on fixational eye movements

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ARTICLE INFO

ABSTRACT

For a behavioral neuroscientist, fixational eye movements are a double-edged sword. On one edge, they make control of visual stimuli difficult, but on the other edge they provide insight into the ways the visual system acquires information from the environment. We have studied macaque monkeys as models for human visual systems. Fixational eye movements of monkeys are similar to those of humans but they are more often vertically biased and spatially more dispersed. Eye movements scatter stimuli from their intended retinal locations, increase variability of neuronal responses, inflate estimates of receptive field size, and decrease measures of response amplitude. They also bias against successful stimulation of extremely selective cells. Compensating for eye movements reduced these errors and revealed a fine-grained motion pathway from V1 feeding the cortical ventral stream. Compensation is a useful tool for the experimenter, but rather than compensating for eye movements, the brain utilizes them as part of its input. The saccades and drifts that occur during fixation selectively activate different types of V1 neurons. Cells that prefer slower speeds respond during the drift periods with maintained discharges and tend to have smaller receptive fields that are selective for sign of contrast. They are well suited to code small details of the image and to enable our fine detailed vision. Cells that prefer higher speeds fire transient bursts of spikes when the receptive field leaves, crosses, or lands on a stimulus, but only the most transient ones (about one-third of our sample) failed to respond during drifts. Voluntary and fixational saccades had very similar effects, including the presence of a biphasic extraretinal modulation that interacted with stimulus-driven responses. Saccades evoke synchronous bursts that can enhance visibility but these bursts may also participate in the visual masking that contributes to saccadic suppression. Study of the small eye movements of fixation may illuminate some of the big problems in vision.

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1. Introduction

Fixational eye movements are the movements that occur when subjects are trying to control their gaze within a restricted location. They occur in a variety of situations and they serve diverse purposes. When scanning a visual scene, fixational eye movements occur for short pauses between the large saccadic eye movements that move the eye from place to place. These fixational pauses consist of unintentional slow drifts and involuntary small saccades while the subject acquires information before deliberately saccading to a new location of interest. Longer periods of fixation occur when performing fine sensorimotor tasks, such as threading a needle. Under these circumstances, tiny fixational saccades may move the gaze between two nearby objects to accomplish a demanding task (e.g. Ko, Poletti, and Rucci (2010), Poletti, Listorti, and Rucci (2013)). A different kind of task involves a subject waiting for something unpredictable to happen at a particular place – for example, when a predator is waiting for a small prey to emerge from a hiding place. Then, fixational drifts and saccades occur while keeping the fovea on target. We call this maintained fixation, and it is the main task that has been employed for physiological studies of fixational eye movements.

This is a focused review of work done in my laboratory and closely related work from other laboratories beginning in the 1970s and continuing to the present day. I apologize in advance to colleagues whose equally valuable contributions may not be discussed adequately in this framework. The emphasis of this review is on understanding how fixational eye movements affect the acquisition of sensory information and how they relate to neural coding in the visual pathway from the retina to the early stages of the visual cortex. Many (perhaps most) behavioral neuroscientists regard fixational eye movements as a nuisance, because they are not under the control of the experimenter. However, they are an integral part of the visual process and we gain important insights by understanding their effects.

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Our story begins with behavioral studies comparing monkey and human fixational eye movements. Next, I describe how fixational eye movements influence descriptions of neuronal response properties, the mapping of visual receptive fields in physiological studies and sampling biases for neuronal cell types. Then, I consider how fixational eye movements contribute to neural coding of specific types of sensory information. Finally, I discuss how extraretinal influences linked to saccades—both voluntary and involuntary—modulate neuronal activity and interact with stimulus-driven responses to determine the input to the rest of the brain and the sensory process. All work was carried out in accordance with the code of Ethics of the World Medical Association (Declaration of Helsinki), including informed consent of human subjects.

2. Macaque monkeys as models for the study of human fixational eye movements

"Macaque" monkeys are members of the Asian genus *Macaca* that has been shown to have color and spatial vision nearly identical to humans (DeValois et al., 1974; DeValois, Morgan, & Snodderly, 1974). Most investigations of eye movements have used *Macaca mulatta*, the rhesus monkey, or *Macaca fascicularis*, also known as the cynomolgous monkey. Although there are measurable differences in some retinal features between these species (Snodderly & Sandstrom, 2008), no important differences in their eye movements have been documented to date.

Skavenski et al. (1975) conducted the first quantitative study of monkey fixational eye movements, using rhesus monkeys with implanted scleral search coils (Robinson, 1963). They showed that the monkeys could learn to control eye position within a long (15 s) fixation trial with a precision similar to humans, but only after extensive training with extremely stringent criteria. However, these conditions are not compatible with physiological investigations and they are not representative of natural vision. To compare performance under less extreme conditions, we measured eye position of humans and *M. fascicularis* monkeys during fixation tasks lasting 1–4 s (Snodderly & Kurtz, 1985). Fixation targets were presented in the dark, and eye position was measured with a dual-Purkinje image eyetracker (Crane & Steele, 1978). The fixation target either dimmed or changed orientation at an unpredictable time. One of the human subjects was trained nonverbally to be sure that performance was controlled by the task, not by instructions.

Monkeys had much greater trial-to-trial dispersion of fixation position on the vertical axis than humans did (see also Motter and Poggio (1984)). This dispersion resulted from less precise control of saccades in the dark environment. The poorer control caused an "upshift" of fixational eye positions in the dark that was seen in the monkeys, but not in humans (Snodderly, 1987). The upshift in the dark was confirmed in two other laboratories (Barash et al., 1998, for *M. fascicularis* and Goffart et al., 2006, for *M. mulatta*) who showed that the upshift occurred with large voluntary saccades and with memory-guided saccades in the dark as well. The fact that the lighted environment and stimulation of the extrafoveal retina was sufficient to eliminate the upshift with minimal effect on horizontal eye position indicates a different influence of the parafoveal retina on the vertical and the horizontal eye movement systems of the monkeys. The separation of the vertical and horizontal oculomotor control systems in the brainstem (Krauzlis, 2008) may predispose these subsystems to receive somewhat different sensory inputs.

Both the monkeys and one of the human subjects in our initial study made smaller, but more frequent saccades in the light. In general, monkey fixational eye positions and eye movements became much more similar to humans when tested in a lighted environment (Snodderly, 1987). However, saccadic displacements (sizes, see below) of the monkeys were still 2–4 times those of

humans, and between-trial standard deviations of mean eye position were 2–7 times as large. During a maintained fixation task, about half the monkeys studied in my lab (Kagan, Gur & Snodderly, 2008; Snodderly, 1987) and in the Horwitz lab (Hass & Horwitz, 2011; Horwitz & Albright, 2003) showed a pattern of upward drift counteracted by downward saccades. This pattern of movements appears to reflect a general tendency for the eyes to drift upward whenever visual stimulation is minimal, such as in total darkness or with a small, isolated fixation target. Apparently, many monkeys cannot completely eliminate the upward drift; consequently, they must make corrective downward saccades to maintain a stable mean eye position. The vertical bias of the monkey eye movements differs from the behavior of most human subjects, who are more likely to exhibit a distribution of drifts and corrective saccades with a horizontal bias or a radial symmetry (e.g. Cherici et al. (2012)).

Saccade control during maintained fixation seems to be a difficult challenge for some individuals, both monkeys and humans. Fig 1 illustrates a phenomenon that I called saccade clusters, in which a fixational saccade (FX) away from the fixation locus is followed with no delay by one or more saccades that counteract it (left column). Upper panels show data from a human subject and lower panels display data from a monkey. This behavior suggests that the first saccade is unwanted, and its effect is canceled immediately by some low-level monitoring network that does not require time for conscious intervention. The saccade cluster executes a looping movement that returns the eye to the vicinity of the mean fixation locus (middle column; see also Fig. 7, and observations by Horwitz and Albright (2003)). Voluntary saccades (VL) elicited by stepping the fixation point do not show such complex waveforms (left column), and they carry the eye in a simple, nearly linear trajectory (right column). Although most researchers refer to all small saccades as "microsaccades", the looping saccades have motivated me to distinguish fixational saccades (when the subject is trying to maintain a steady gaze) from voluntary ones (when the subject is instructed to shift gaze to another point). A voluntary saccade and a fixational saccade cluster may have very different net displacement even though they cause comparable maximum displacement. The complex waveforms of the fixational saccade clusters are not an artifact of the eyetracker nor are they limited to subjects whose heads are fixed. Similar waveforms can be seen in records from subject RS with a magnetic search coil and the head free (Fig. 5 of Skavenski et al., 1979; reproduced more clearly as Fig. 2 of Steinman et al., 1982).

For larger voluntary saccades, waveforms recorded with the dual Purkinje image eyetracker display an "overshoot" that is caused by inertial lag and oscillation in the movement of the lens as the eye moves abruptly to a new position (Deubel & Bridgeman, 1995a; Tabernero & Artal, 2014). However, for smaller voluntary saccades in the size range of fixational saccades (<1°), Fig. 1 shows that the "overshoots" are minimal, consistent with the principle that inertial forces on the lens should be reduced for small saccades. It seems likely that some of the data for small saccades in Fig. 5 of Deubel and Bridgeman (1995a) that imply overshoots as large as the saccade, may instead represent looping back-to-back saccades of the type illustrated here. Given that inertial motions of the lens are accompanied by perceptual disturbances (Deubel & Bridgeman, 1995b) it is functionally advantageous that the lens motions are negligible during small saccades that may occur during demanding visual tasks.

Publications from my lab have either reported both net and maximum displacements (Snodderly, 1987), or only maximum displacements (Kagan et al., 2008; Snodderly, Kagan, & Gur, 2001). Other laboratories have often reported the net displacement only (e.g. Chen and Hafed (2013), Horwitz and Albright (2003)), so readers will need to make comparisons with care. The examples here of