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Suppressive interactions underlying visually evoked fixational saccades

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ABSTRACT

Small saccades occur frequently during fixation, and are coupled to changes in visual stimulation and cognitive state. Neurophysiologically, fixational saccades reflect neural activity near the foveal region of a continuous visuomotor map. It is well known that competitive interactions between neurons within visuomotor maps contribute to target selection for large saccades. Here we asked how such interactions in visuomotor maps shape the rate and direction of small fixational saccades. We measured fixational saccades during periods of prolonged fixation while presenting pairs of visual stimuli (parafoveal: 0.8° eccentricity; peripheral: 5° eccentricity) of various contrasts. Fixational saccade direction was biased toward locations of parafoveal stimuli but not peripheral stimuli, ~100–250 ms following stimulus onset. The rate of fixational saccades toward parafoveal stimuli (congruent saccades) increased systematically with parafoveal stimulus contrast, and was suppressed by the simultaneous presentation of a peripheral stimulus. The suppression was best characterized as a combination of two processes: a subtractive suppression of the overall fixational saccade rate and a divisive suppression of the direction bias. These results reveal the nature of suppressive interactions within visuomotor maps and constrain models of the population code for fixational saccades.

1. Introduction

Small (<1–2°) saccades occur 1–2 times per second during fixation (Ditchburn & Ginsborg, 1953; Martinez-Conde, Macknik, & Hubel, 2004; Martinez-Conde, Otero-Millan, & Macknik, 2013; Ratliff & Riggs, 1950; Rolfs, 2009; Steinman et al., 1973; Zuber, Stark, & Cook, 1965). The function of these small, fixational saccades for vision has prompted much investigation; they might serve to counter visual fading (Engbert & Mergenthaler, 2006; Martinez-Conde et al., 2006), correct fixation error (Cornsweet, 1956; Engbert & Kliegl, 2004; Engbert & Mergenthaler, 2006; Guerrasio et al., 2010), and/or sample visual information at a fine spatial scale (Ko, Poletti, & Rucci, 2010; McCamy et al., 2014; Otero-Millan et al., 2013; Rucci et al., 2007). The rate and direction of fixational saccades are modulated by sensory processes. For example, the rate of fixational saccades (as well as large saccades) decreases following a visual transient, a phenomenon called "microsaccadic/saccadic inhibition" (Reingold & Stampe, 2002; Rolfs, Kliegl, & Engbert, 2008; Stampe & Reingold, 2002; Valsecchi & Turatto, 2007). The rate and direction of fixational saccades are also modulated by cognitive processes, including covert shifts of attention (Brien et al., 2009; Cui et al., 2009; Engbert & Kliegl, 2003; Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Laubrock et al., 2010; Pastukhov & Braun, 2010; Poletti, Listorti, & Rucci, 2013; Rolfs, Engbert, & Kliegl, 2004, 2005) (see Section 4.1).

Fixational saccades are motor expressions of neural activity on a continuous visuomotor map. The superior colliculus (SC), for example, topographically encodes the direction and amplitude of saccades (Carello & Krauzlis, 2004; McPeek & Keller, 2004; Robinson, 1972; Sparks, Holland, & Guthrie, 1976; Wurtz & Goldberg, 1972) and locations of behavioral relevance in the environment, including the locus of attention (Fecteau, Bell, & Munoz, 2004; Ignashchenkova et al., 2003; Lovejoy & Krauzlis, 2010; Müller, Philiastides, & Newsome, 2005). In particular, neurons in the rostral pole of the SC are selective for the direction and amplitude of fixational saccades (Hafed, Goffart, & Krauzlis, 2009; Hafed & Krauzlis, 2012). Nonlinear competitive interactions have been well documented in the responses of SC neurons in a variety of species (Basso & Wurtz, 1997; Hafed & Ignashchenkova, 2013; Li & Basso, 2005; Munoz & Istvan, 1998; Munoz & Wurtz, 1993; Mysore, Asadollahi, & Knudsen, 2010; Vokoun et al., 2014). The responses of a neuron to a stimulus inside its response field (RF) are reduced by the simultaneous presentation of a second

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stimulus, either also inside the RF (Li & Basso, 2005) or spatially far apart (Basso & Wurtz, 1997, 1998). The nature of these competitive interactions between SC neurons has been modeled using weighted averaging and divisive normalization (e.g., Vokoun et al., 2014). These neural response properties have been shown to underlie a number of behavioral metrics in humans and monkeys, including the rate and direction of large saccades. The rate and direction of fixational saccades, therefore, might provide a complementary characterization of the competitive interactions in visuomotor maps.

We used visual stimulation as an experimental manipulation, and quantified how fixational saccades depended on interactions between pairs of visual stimuli. The task was to maintain fixation on a small central marker. A parafoveal stimulus was presented either alone or simultaneously with a peripheral stimulus. The contrast of the peripheral stimuli (when present) was held constant, while the contrast of the parafoveal stimuli was systemically varied. We measured saccade rate and direction during an epoch 100–250 ms after stimulus onset, i.e., a time interval during which microsaccadic/saccadic inhibition has been reported. We limited our analyses to small saccades (<2°), which we defined as fixational saccades, i.e., saccades that occurred while observers were instructed to fixate centrally. Some of these saccades may have shifted gaze to the parafoveal stimuli. We adopted the term "fixational saccades" to avoid debate on the precise classification of microsaccades and their purpose; our present conclusions do not depend on distinguishing microsaccades from small, exploratory saccades.

We found that fixational saccades were biased toward the parafoveal stimuli, but they were suppressed by the simultaneous presentation of the peripheral stimuli. The suppression was best characterized as a combination of two separate processes: a subtractive suppression of the overall fixational saccade rate and a divisive suppression of the direction bias. Specifically, there was a reduction in the overall rate of fixational saccades, similar to previous reports of microsaccadic/saccadic inhibition, when parafoveal stimuli were paired with a peripheral stimulus compared to when parafoveal stimuli were presented alone. This reduction in overall fixational saccade rate was independent of parafoveal contrast and was modeled as subtractive. In addition, the relative proportion of fixational saccades toward parafoveal stimuli increased with parafoveal contrast, but less so when they were paired with a peripheral stimulus. This process was modeled as divisive. The divisive suppression of the direction bias could not be explained by the change in overall rate. We conclude that the suppression of fixational saccades induced by visual stimulation can be decomposed into two component processes, one subtractive and the other divisive, and we propose a framework in which these computational processes are performed in a visuomotor map like that in the SC.

2. Materials and methods

2.1. Observers

Eight observers (three females, aged 24–33) with normal or corrected-to-normal vision participated in the study, including one of the authors. Three observers wore glasses while participating in the study. Six were experienced psychophysical observers. Observers provided written informed consent, and the experimental protocol was approved by the University Committee on Activities involving Human Subjects at New York University. This work was carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Apparatus, stimuli, and experimental procedure

Observers sat in the dark and were instructed to maintain fixation on a small gray central marker on a dark screen (0.2° diameter; 15.2 cd/m^2; Weber contrast 1) for the duration of each experimental block, with head positioned on a chin rest to avoid large head movements that might cause artifacts in saccade detection. There was no additional task. Eye movements were recorded (1000 Hz, monocular) with an Eyelink 1000 infrared eye tracker (SR Research Ltd., Ontario, Canada) with a spatial resolution of 0.01° from sensor noise and 0.25–0.5° average accuracy when using a chin rest. A 9-point (grid) calibration was performed and validated at the start of each experimental block.

Stimuli were brief presentations of white, circular spots on a dark background (7.5 cd/m^2). The spots appeared at two eccentricities (0.8° and 5°; "parafoveal" and "peripheral", respectively) and one of the four cardinal locations (above, below, left or right of fixation) (Fig. 1A). There were four trial types: blank, parafoveal-alone, peripheral-alone, and paired parafoveal and peripheral. During the parafoveal-alone trials, a parafoveal stimulus (0.4° diameter) was presented at one of the four 0.8° locations. During the peripheral-alone trials, a peripheral stimulus (0.6° diameter) was presented at one of the four 5° locations. During the paired trials, a parafoveal stimulus was presented simultaneously with one of the peripheral stimuli (16 location combinations). Each stimulus was presented for 80 ms, followed by an inter-stimulus interval of 480 ms. A trial epoch (560 ms) was defined as a stimulus presentation plus an inter-stimulus interval, beginning with the onset of the stimulus. Some trials were blank, during which no stimulus was presented, while the fixation marker remained on the screen. Parafoveal stimulus location and contrast varied across trials (luminances: 8.3–75.4 cd/m^2; Weber contrasts: 0.1–9) in randomly shuffled order. The peripheral stimuli, when present, were held at a constant contrast (luminance 37.6 cd/m^2; Weber contrast 4). Each experimental block consisted of 480 trials (269 s). Each observer completed multiple experimental blocks spanning several days, yielding 13,000–20,000 trials per observer.

Stimuli were generated using MATLAB (Mathworks, MA) and MGL (http://justingarner.net/mgl) on a Macintosh computer and displayed on a 22″ flat-screen CRT monitor (Hewlett-Packard p1230; resolution: 1152 × 870; refresh rate: 75 Hz) at a distance of 57 cm. The MGL Eyelink toolbox interfaced with the eye tracker. The monitor provided approximately 39° × 30° viewing angle. The display was calibrated and gamma-corrected using a linearized lookup table.

2.3. Saccade detection

Raw gaze positions were converted into degrees of visual angle, based on the 9-point (grid) calibration that was performed at the start of each experimental block. Blink intervals were defined according to the Eyelink blink detection algorithm along with samples from 200 ms preceding to 350 ms following each Eyelink-detected blink interval. Sample values during blink intervals were ignored for all subsequent analyses.

Saccades were detected using an established algorithm that compares eye-movement velocity with a threshold (Engbert & Kliegl, 2003; Engbert & Mergenthaler, 2006). The entire eye position trace from each block (after blink removal) was used for setting a saccade-detection velocity-threshold. A threshold criterion for saccade detection was determined based on the 2D (horizontal and vertical) eye-movement velocity during the block. Specifically, we set the threshold to be 7 times the standard deviation of the 2D eye-movement velocity, using a median-based estimate of the standard deviation (Engbert & Kliegl, 2003). A saccade was identified when the eye-movement velocity exceeded this threshold for