Target frequency influences antisaccade endpoint bias: Evidence for perceptual averaging

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ABSTRACT

Perceptual judgments related to stimulus-sets are represented computationally different than individual items. In particular, the perceptual averaging hypothesis contends that the visual system represents target properties (e.g., eccentricity) via a statistical summary of the individual targets included *within* a stimulus-set. Here we sought to determine whether perceptual averaging governs the visual information mediating an oculomotor task requiring top-down control (i.e., antisaccade). To that end, participants completed antisaccades (i.e., saccade mirror-symmetrical to a target) – and complementary prosaccades (i.e., saccade to veridical target location) – to different target eccentricities (10.5°, 15.5° and 20.5°) located left and right of a common fixation. Importantly, trials were completed in blocks wherein eccentricities were presented with equal frequency (i.e., control condition) and when the 'proximal' (10.5°: i.e., proximal-weighting condition) and 'distal' (20.5°: i.e., distal-weighting condition) targets were respectively presented five times as often as the other eccentricities. If antisaccades are governed by a statistical summary then amplitudes should be biased in the direction of the most frequently presented target within a block. As expected, pro- and antisaccade across each target eccentricity were associated with an undershooting bias and prosaccades were refractory to the manipulation of target frequency. Most notably, antisaccades in the proximal-weighting condition had a larger undershooting bias than the control condition, whereas the converse was true for the distal-weighing condition; that is, antisaccades were biased in the direction of the most frequently presented target. Thus, we propose that perceptual averaging extends to motor tasks requiring top-down cognitive control.

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1. Introduction

The most frequent motor act that humans perform is an eye movement that brings the fovea to a target of interest (i.e., prosaccade). In fact, an individual can make upwards of 100,000 prosaccades on a daily basis (Irwin & Carlson-Radvansky, 1996). Notably, the direct spatial relations between stimulus and response permit absolute visual information to mediate prosaccade sensorimotor transformation via retinotopically organized motor maps within the superior colliculus (Wurtz & Albano, 1980). In spite of the direct spatial relations, primary and secondary (i.e., corrective) prosaccades typically undershoot veridical target location (Abrams, Meyer, & Kornblum, 1989; Becker & Fuchs, 1969; Deubel, Wolf, & Hauske, 1986; Gillen, Weiler, & Heath, 2013;

Prablanc & Jeannerod, 1975; Robinson, 1964; Weber & Daroff, 1971). In particular, prosaccades exhibit a 10% undershooting bias that is thought to reflect an invariant control strategy that minimizes saccade flight time (i.e., saccadic flight time hypothesis: Harris, 1995) and/or the energy requirements of the response (i.e., energy minimization hypothesis: Becker, 1989). Indeed, undershooting represents an optimal strategy for prosaccades because it reduces the potential of an overshooting error and the time-consuming and energy-demanding requirements of implementing a corrective response in a direction opposite to the primary saccade (Becker, 1989; Harris, 1995; see also Elliott et al., 2004).

In contrast to prosaccades, antisaccades require decoupling the spatial relations between stimulus and response and implementing a saccade to a target's mirror-symmetrical location (i.e., 180° spatial transformation). As such, antisaccades provide a framework for understanding how top-down and cognitive control influences motor output. Extensive work has shown that antisaccades produce longer reaction times (RT) than prosaccades (Fischer &

Weber, 1992; Hallett, 1978) – a behavioral 'cost' that has been related to the time-consuming processes of suppressing of a stimulus-driven prosaccade (i.e., response suppression) and the *visual* remapping of a target's spatial properties (i.e., vector inversion) (for extensive review see Munoz & Everling, 2004). Moreover, it is not surprising that antisaccades are less accurate and more variable than prosaccades (Dafoe, Armstrong, & Munoz, 2007; Evdokimidis, Tsekou, & Smyrnis, 2006; Heath et al., 2011; Krappmann, Everling, & Flohr, 1998); after all, decoupling the spatial relations between stimulus and response does not permit direct sensorimotor transformation via retinotopically organized motor maps in the superior colliculus. Instead, vector inversion requires that a *relative* target percept support sensorimotor transformations. In other words, the top-down control of antisaccades influences the nature of the visual information supporting motor output.[1]

As mentioned above, prosaccades exhibit an invariant undershooting bias; however, antisaccades are associated with a target-specific bias based on the eccentricities included within a stimulus-set. For example, Dafoe, Armstrong, and Munoz (2007) and Evdokimidis, Tsekou, and Smyrnis (2006) reported that the 'proximal' and 'distal' targets within their stimulus-sets respectively over- and undershot veridical target location, whereas their central targets exhibited a null bias (Dafoe et al. 0.5°, 1.0°, 2.0°, 4.0° and 8.0°; Evdokimidis et al. 2.0°, 3.0°, 4.0°, 5.0°, 6.0°, 7.0°, 8.0°, 9.0° and 10.0°) (see also Bell, Everling, & Munoz, 2000; Heath et al., 2011; Weiler & Heath, in press; Weiler et al., 2011). One interpretation of this finding is that the visual percept supporting antisaccades overestimates 'proximal' targets and underestimates 'distal' targets *within* a stimulus-set (i.e., the range effect hypothesis: see Kapoula, 1985; Poulton, 1981). We (Gillen & Heath, in press) recently sought to test the range effect hypothesis by having participants antisaccade in separate blocks (i.e., proximal and distal) that contained the same number of target eccentricities but differed with respect to their magnitudes. In the proximal block, target eccentricities were 3.0°, 5.5°, 8.0°, 10.5° and 13.0°, whereas in the distal block target eccentricities were 10.5°, 13.0°, 15.5°, 18.0° and 20.5°. In line with Dafoe et al. and Evdokimids et al., the proximal block showed that the 'proximal' (i.e., 3.0°, 5.5°) and 'distal' (i.e., 10.5°, 13.0°) targets were respectively over- and undershot, whereas responses to the central target (8.0°) did not reliably differ from veridical. In contrast, the distal block showed an undershooting bias that was independent of target eccentricity. Most notably, that the target eccentricities common to each block (i.e., 10.5° and 13.0°) produced an undershooting bias directly counters the range effect hypothesis' assertion that the 'proximal' and 'distal' targets within a stimulus-set respectively over- and undershoot veridical target location. To account for our findings, we drew upon the perceptual averaging hypothesis' assertion that the properties of a stimulus-set (e.g., extent, size, luminance) are rapidly summarized without precise information about individual targets (Albrecht, Scholl, & Chun, 2012; Ariely, 2001; Chong & Treisman, 2003; Davarpanah Jazi & Heath, 2014). For example, Ariely reported that although participants were unable to identify whether an individual circle was a member of a stimulus-set, they were able to accurately represent the average size of all circles included in the set. Indeed, such a strategy is thought to diminish task-based attentional demands when a performer is unable to predict when an individual member of a stimulus-set will be presented. In the context of our previous work, we proposed that the top-down nature of antisaccades rendered the mediation of target eccentricity via a statistical summary (i.e., the average) of the range

of eccentricities included in each stimulus-set. Accordingly then, the statistical summary for the proximal and distal block corresponded to each block's central target. As such, the fact that antisaccades to the central target in the proximal block (i.e., 8.0°) did not reliably differ from veridical, whereas the 'proximal' and 'distal' targets respectively over- and undershot target location demonstrates that amplitudes were, in part, mediated via a statistical summary. In turn, because the percept supporting antisaccades exhibits an increased undershooting bias with increasing target eccentricity (Dafoe, Armstrong, & Munoz, 2007; Evdokimidis, Tsekou, & Smyrnis, 2006), the reliable and large magnitude undershooting associated with the distal block's central target (i.e., 15.5°) resulted in a similar bias for the other target eccentricities included within the block. In other words, perceptual averaging asserts that the endpoint bias (or lack thereof) associated with a stimulus-set's central target (i.e., the statistical summary) determines the *direction* and *magnitude* of the endpoint bias for the individual targets included within the set.

The goal of the present investigation was to directly test the assertion that perceptual averaging influences the nature of the visual information supporting antisaccades. To accomplish that objective, participants completed antisaccades – and complementary prosaccades – to three target eccentricities (10.5°, 15.5° and 20.5°) located left and right of a central fixation in conditions that differed with regard to the frequency individual target eccentricities were presented. In the *control condition*, target eccentricities were presented with equal frequency. In the *proximal-weighting* condition, the 'proximal' target eccentricity (10.5°) was presented five times as often as the other target eccentricities, whereas in the *distal-weighting* condition the 'distal' target eccentricity (20.5°) was presented five times as often as the other target eccentricities. We are aware that previous work has shown that probabilistic information related to the spatial location of a target (i.e., left or right and/or above or below a central fixation) influences pro- and antisaccade reaction times – a finding that has been linked to improved target detection and increased pre-saccadic collicular buildup neuron firing rates in the receptive field of the frequently presented target (Dorris & Munoz, 1998; Geng & Behrmann, 2005; Liu et al., 2010; see also Gmeindl, Rontal, & Reuter-Lorenz, 2005). Notably, however, the current study differs from previous work in that we were interested in determining whether the frequent presentation of a target eccentricity influences antisaccade endpoint bias. Indeed, if the perceptual averaging hypothesis is correct, then the proximal- and distal-weighting conditions should render statistical summaries – and associated visual percepts – that are biased in the direction of the most frequently presented target. More specifically, it is predicted that amplitudes for each target eccentricity in the proximal-weighting condition will undershoot veridical target location more than their matched target eccentricities in the control condition. In turn, the converse pattern is predicted for the distal-weighting condition; that is, responses will produce a decreased undershooting bias compared to the control condition. Last, and as indicated above, we included prosaccades to the same target eccentricities and conditions as used for antisaccades. Prosaccades were included to demonstrate that responses mediated via absolute visual information are refractory to context-dependent manipulations (i.e., frequency) of target eccentricity.

2. Methods

2.1. Participants

Twenty participants from the University of Western Ontario community volunteered for the present study (11 females and 9

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[1] The sensorimotor transformation supporting antisaccades are not based on absolute target eccentricity; rather, they are supported via visual information related to perceived target eccentricity.