



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-weighting 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 &

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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 Evdokimidis 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 anti-saccades 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

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.

males; age range = 19–29 years). All participants had normal or corrected-to-normal vision. This research was conducted in accordance with the Declaration of Helsinki and all participants signed a consent form approved by the Office of Research Ethics, The University of Western Ontario.

2.2. Apparatus and procedures

Participants sat comfortably at a normal tabletop (height = 770 mm) with their head placed in a head-chin rest for the duration of data collection. Visual stimuli were presented on a 30-inch LCD monitor (60 Hz, 8 ms response rate, 1280 × 960 pixels; Dell 3007WFP, Round Rock, TX, USA) located at a viewing distance 550 mm from the participant and centered on their midline. The gaze location of participant's left eye was sampled at 360 Hz using a video-based eye recording system (Eye-Trac6: Applied Sciences Laboratories, Bedford, MA, USA). Prior to data collection, a nine-point calibration of the participant's viewing space was completed. Two computer monitors that were visible only to the experimenter provided real-time point of gaze information, trial-by-trial saccade kinematics (e.g., displacement, velocity), and information related to the accuracy of the eye tracking system (i.e., to perform recalibration when necessary). Computer events and the presentation of visual stimuli were controlled via MATLAB (7.8.0: The Math Works, Natick, MA, USA) and the Psychophysics Toolbox extensions (ver 3.0; see Brainard, 1997). The lights in the experimental suite were extinguished throughout data collection.

Visual stimuli were presented against a high-contrast black background and included a white fixation cross (1° and 135 cd/m^2) centered horizontally on the monitor and yellow target crosses (1° and 127 cd/m^2) presented 10.5° (i.e., 'proximal' target), 15.5° ('middle' target), and 20.5° (i.e., 'distal' target) left and right of fixation. Stimuli were located on the horizontal meridian and at the participant's eye level. Each trial began with the presentation of the white fixation cross which alerted the participant to direct their gaze to its location. After a stable fixation was achieved ($\pm 1.5^\circ$ for 420 ms), a randomized foreperiod (1000–2000 ms) was introduced during which time the fixation cross remained visible. Following the foreperiod, a target stimulus was briefly (i.e., 50 ms) presented and its onset cued participants to pro- or antisaccade "as quickly and as accurately as possible." The fixation cross and target were concurrently extinguished (i.e., overlap paradigm). Prosaccades required a response to veridical target location, whereas antisaccades required a response mirror-symmetrical to the target. The 50 ms target presentation was used so that the target was unavailable throughout response planning and execution – a method requiring visual vector inversion for antisaccades as opposed to a continuous target presentation wherein antisaccades may be mediated via an obligatory shift of attention from the target to a homologous region in space (Olk & Kingstone, 2003).

Pro- and antisaccades were completed across conditions that differed with respect to the weighting of target eccentricity (Fig. 1). In the *control condition*, an equal number of trials (i.e., 10) were completed to each target eccentricity by visual space combination (i.e., 60 pro- and antisaccade trials). In the *proximal-weighting* condition, the 'proximal' target (i.e., 10.5°) was presented five times as often as the 'middle' (i.e., 15.5°) and 'distal' (i.e., 20.5°) target eccentricities. Thus, 50 trials were completed to each left and right visual field 'proximal' target, and 10 trials were completed to each left and right visual field 'middle' and 'distal' target. In the *distal-weighting* condition, the 'distal' target was presented five times as often as the 'proximal' and 'middle' target eccentricities. As such, 50 trials were completed to each left and right visual field 'distal' target, whereas 10 trials were completed to each left and right visual field 'proximal' and 'middle' target. Therefore,

140 pro- and antisaccade trials were performed in each of the proximal- and distal-weighting conditions.

The three weighting conditions (i.e., control, proximal-weighting, distal-weighting) were completed in separate sessions with each separated by a minimum of 24 h. We employed the separate sessions in order to minimize eye strain and mental fatigue. All participants performed the control condition during the first session, whereas the ordering of the proximal- and distal-weighting conditions was counterbalanced across the remaining sessions. Notably, within each weighting condition pro- and antisaccades were performed in separate and counterbalanced blocks, and prior to each block participants received written instructions related to the nature of the task (prosaccade vs. antisaccade). The ordering of target presentation (visual space by target eccentricity) was randomized. During data collection a trial associated with signal loss (e.g., eye-blink) was deleted and re-entered into the trial matrix.

2.3. Data analysis

Displacement data were filtered offline using a dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Filtered displacement data were used to compute instantaneous velocities via a five-point central finite difference algorithm. Acceleration data were similarly obtained from the velocity data. Saccade onset was marked when velocity and acceleration values exceeded $30^\circ/\text{s}$ and $8000/\text{s}^2$, respectively. Saccade offset was marked when saccade velocity fell below a threshold value of $30^\circ/\text{s}$ for 15 consecutive frames (i.e., 42 ms).

2.4. Dependent variables and statistical analyses

The dependent variables were saccade amplitude in the primary (i.e., horizontal) movement direction and reaction time (RT: time from stimulus presentation to saccade onset). RT data were removed due to: (1) RT greater than two standard deviations above the mean group performance (i.e., $\text{RT} > 650 \text{ ms}$, and $< 1\%$ of trials), and (2) An anticipatory response (i.e., $\text{RT} < 85 \text{ ms}$, and $< 2\%$ of trials) (Wenban-Smith & Findlay, 1991). As well, trials involving a directionally incorrect response (i.e., antisaccade to veridical target location instead of the mirror-symmetrical location, or vice versa) were excluded from the RT and amplitude analyses: less than 1% and 5% of trials were removed due to pro- or antisaccade directional errors, respectively. The low antisaccade error rate is attributed to the use of an overlap paradigm and the completion of pro- and antisaccades in separate blocks. Post hoc decompositions for pro- and antisaccades were completed via paired-samples *t*-tests, whereas the decomposition of target eccentricity was computed via power polynomials (i.e., trend analysis: see Pedhazur, 1997). Only significant effects are reported below ($p < 0.05$).

3. Results

3.1. Pro- and antisaccade amplitudes

Our first analysis examined amplitudes via 2 (task: pro-, antisaccade) by 2 (visual field: left, right) by 3 (weighting condition: control condition, proximal-weighting, distal-weighting) by 3 (target eccentricity: 'proximal' [10.5°], 'middle' [15.5°], 'distal' [20.5°]) repeated measures ANOVA. Results produced main effects for task, $F(1, 19) = 57.04$, $p < 0.001$, weighting condition, $F(2, 38) = 17.48$, $p < 0.001$, target eccentricity, $F(2, 38) = 951.05$, $p < 0.001$, and interactions involving task by weighting condition, $F(2, 38) = 20.36$, $p < 0.001$, and task by target eccentricity, $F(2, 38) = 298.16$, $p < 0.001$. In terms of the task by weighting condition interaction, antisaccades, $F(2, 38) = 24.46$, $p < 0.001$, but not prosaccades,

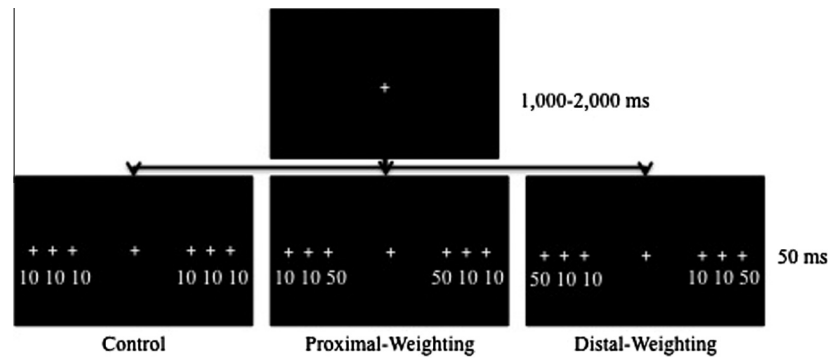


Fig. 1. Schematic representation of the visual stimuli and target eccentricity weighting conditions. A central fixation was presented for a randomized foreperiod after which a target stimulus was presented left or right of fixation. For the purposes of this figure each target eccentricity is displayed to show the frequency by which individual eccentricities were presented within control, proximal- and distal-weighting conditions (i.e., the numerical value below each target indicates the frequency of its presentation). Target onset served as the response imperative and both target and fixation were extinguished 50 ms later. Note: targets were presented as yellow crosses but are rendered as white for the purposes of this figure.

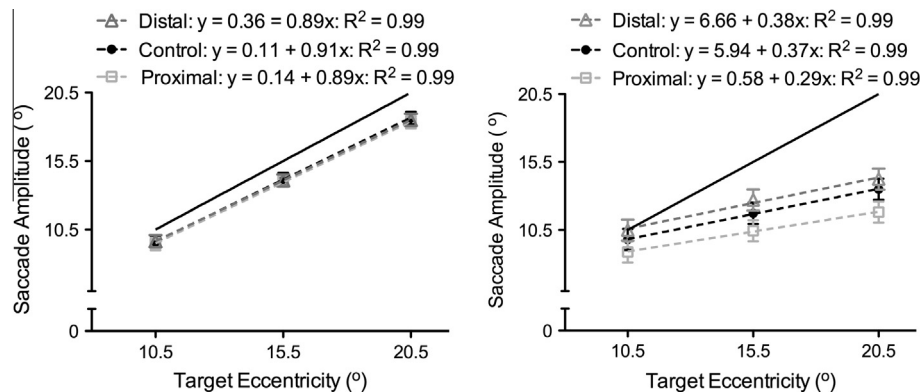


Fig. 2. Mean pro- (left panel) and antisaccade (right panel) amplitudes ($^{\circ}$) as a function of weighting condition and target eccentricity and their respective linear regression equations. Black closed circles, light gray open squares, and dark gray open triangles represent control, proximal- and distal-weighting conditions, respectively. The solid line in each panel represents veridical target location, whereas the hatched lines represent the linear regression for each weighting condition to target eccentricity. Error bars represent the 95% within-participants confidence intervals (Loftus & Masson, 1994).

$F(2,38) = 0.72$, $p = 0.50$, were reliably influenced by the different weighting conditions. In particular, Fig. 2 shows that antisaccade amplitudes for the proximal-weighting condition were less than the control condition ($t(19) = -3.75$, $p < 0.001$), whereas amplitudes for distal-weighting condition were greater than the control condition ($t(19) = 6.24$, $p < 0.001$). Moreover, the bottom panels of Fig. 3 present difference scores (computed separately for pro- and antisaccades) contrasting proximal- and distal-weighting conditions to the control condition (e.g., proximal-weighting condition antisaccade minus control condition antisaccade). The figure shows that antisaccade amplitudes in the proximal- and distal-weighting conditions were respectively less than and greater than their control condition counterpart, whereas prosaccade amplitudes did not vary as a function of weighting condition. In other words, antisaccade amplitudes scaled in relation to the most frequently presented target included in a block. In terms of the task by target eccentricity interaction, pro- and antisaccades amplitudes increased in relation to increasing target eccentricity (only linear effects significant: $F_s(1,19) = 3207.31$ and 140.57 , respectively for pro- and antisaccades, $p_s < 0.001$). To further decompose the interaction, we first contrasted pro- and antisaccade amplitudes separately for matched target eccentricities and subsequently computed participant-specific slopes relating pro- and antisaccade amplitudes to target eccentricity. Pro- and antisaccade amplitudes to the 'proximal' target did not reliably differ, $t(19) = -0.50$, $p = 0.62$; however, antisaccade amplitudes to the

'middle' and 'distal' targets were less than their prosaccade counterparts ($t_s(19) > -7.65$, $p_s < 0.001$). Additionally, antisaccades produced a shallower slope (0.35° , $CI_{95\%} = 0.06$) than prosaccades (0.89° , $CI_{95\%} = 0.06$), $t(19) = 19.14$, $p < 0.001$ (Fig. 2).²

Fig. 2 provides qualitative evidence that pro- and antisaccades across each block and weighting condition undershot veridical target location. To directly address this issue, the top panels of Fig. 3 present difference scores relating pro- and antisaccade amplitudes to veridical target location (i.e., prosaccade [antisaccade] amplitude minus veridical target location) for each weighting condition and target eccentricity combination. Notably, the top panels of Fig. 3 demonstrate that pro- and antisaccades reliably undershot target location independent of weighting condition and target eccentricity ($t_s(19) > -6.60$, $p_s < 0.001$). As well, Fig. 3 shows that the magnitude of the antisaccade undershooting bias increased with increasing target eccentricity.

3.2. Pro- and antisaccade RTs

RT data were subjected to the same ANOVA model as described above and elicited main effects for task, $F(1,19) = 122.42$, $p < 0.001$, and weighting condition, $F(2,38) = 7.32$, $p < 0.01$. RTs for antisac-

² Here and elsewhere confidence intervals are computed as a function of within-participants variability (Loftus & Masson, 1994).

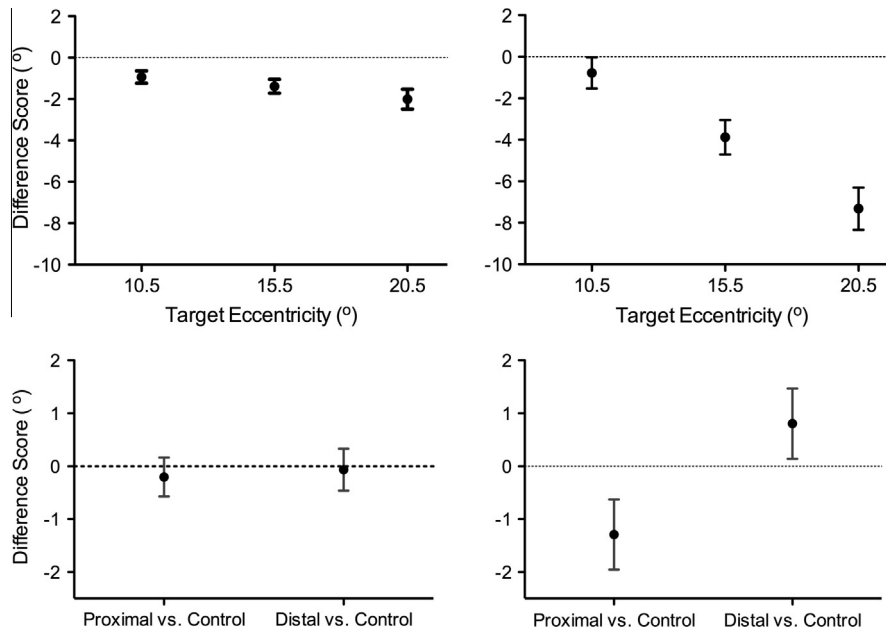


Fig. 3. The top panels depict mean target eccentricity-specific differences scores (°: amplitude minus vertical target location) for pro- (left panel) and antisaccades (right panel). The bottom panels depict weighting-condition specific difference scores (°: proximal-weighting condition minus control condition; distal-weighting condition minus control condition) computed separately for pro- (left panel) and antisaccades (right panel). For all panels, errors bars represent 95% confidence intervals. The absence of overlap between error bars and zero (i.e., the horizontal dotted line) represents a reliable difference that can be interpreted mutually inclusive to a test of the null hypothesis (Cumming, 2013).

cadetes (295 ms, $CI_{95\%} = 29$) were longer than prosaccades (221 ms, $CI_{95\%} = 29$), and control condition RTs (269 ms, $CI_{95\%} = 19$) were longer than proximal- (249 ms, $CI_{95\%} = 19$) or distal-weighting (256 ms, $CI_{95\%} = 19$) conditions ($t(19) = 3.57$ and 2.64 , $ps < 0.03$), which did not differ ($t(19) = -1.27$, $p = 0.22$) (Fig. 4).

To determine if saccade amplitudes were influenced by a planning-related speed-accuracy trade-off, we computed correlation coefficients separately for pro- and antisaccades based on mean participant performance for each target eccentricity and weighting condition combination. For prosaccades, Table 1 shows that the 'proximal' and 'distal' targets in the control condition, the 'proximal' target in the proximal- and distal-weighting conditions, and the 'middle' target in the distal weighting-condition produced a reliable – and negatively correlated – relationship between RT and amplitude; however, the remaining weighting condition and target eccentricity combinations did not ($ps > 0.05$). For antisaccades, RT and amplitude did not elicit a reliable relationship. Thus,

Table 1

Correlation coefficients and p -values for the relationship between pro- and antisaccade reaction times and amplitudes in the control, proximal- and distal-weighting conditions.

Target eccentricity (°)	Prosaccade		Antisaccade	
	R-value	p-value	R-value	p-value
<i>Control</i>				
10.5	-0.72	0.000	-0.25	0.287
15.5	-0.38	0.100	0.15	0.566
20.5	-0.55	0.011	0.07	0.803
<i>Proximal weighting</i>				
10.5	-0.69	0.000	-0.13	0.587
15.5	-0.23	0.320	-0.18	0.438
20.5	-0.33	0.160	-0.18	0.478
<i>Distal weighting</i>				
10.5	-0.50	0.025	-0.12	0.607
15.5	-0.50	0.025	-0.06	0.793
20.5	-0.32	0.166	0.12	0.616

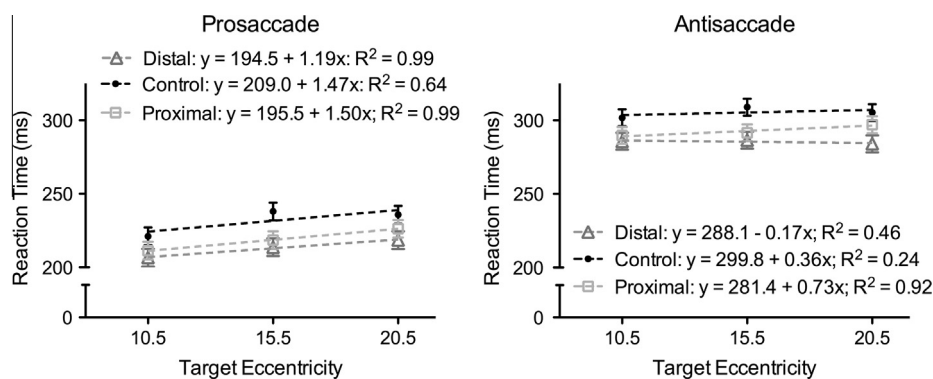


Fig. 4. Mean pro- (left panel) and antisaccade (right panel) reaction times (ms) as a function of weighting-condition and target eccentricity. The lines in each panel represent linear regressions, and associated regression equations are reported in each panel. Error bars represent the 95% within-participants confidence intervals (Loftus & Masson, 1994).

planning times were neither reliably nor consistently related to pro- or antisaccade amplitudes.

4. Discussion

4.1. Pro- and antisaccades, and the manipulation of target frequency influences response latencies

Antisaccades yielded longer RTs than prosaccades. This well-documented finding is taken to evince the additional time required to suppress a stimulus-driven prosaccade (i.e., response suppression) and invert a target's spatial location to mirror-symmetrical space (i.e., vector inversion) (Hallett, 1978; for review see Munoz & Everling, 2004). Additionally, proximal- and distal-weighting conditions produced shorter RTs than the control condition independent of task (i.e., pro-, antisaccade) and target eccentricity. Recall that previous studies have shown that the frequent presentation of a target in a specific visual field (e.g., left or right and/or above or below a central fixation) results in shorter RTs for the most frequently presented visual field (Geng & Behrmann, 2005; Gmeindl, Rontal, & Reuter-Lorenz, 2005; Liu et al., 2010; Liu et al., 2011) – a finding attributed to improved pre-saccade motor preparation (Dorris & Munoz, 1998; see also Rolfs & Vitu, 2007). In contrast to previous work, we manipulated the frequency of target eccentricity independent of the visual field (i.e., left, right) the target was presented. In spite of the difference in methodology between our work and previous studies, it is possible that the manipulation of target eccentricity favoured pre-saccade motor preparation. As such, the shorter RTs associated with the proximal- and distal-weighting conditions may relate to an increased frequency of express saccades (i.e., latencies with a peak distribution of ~100 ms: Fischer & Ramsperger, 1984; see also Rolfs & Vitu, 2007). In addressing this issue, we examined pro- and antisaccade RT distributions (including directionally incorrect saccades) for control, proximal- and distal-weighting conditions. As shown in Fig. 5, neither the proximal- nor distal-weighting conditions elicited a separate express-saccade peak – a finding that was consistent across pro- and antisaccades. Thus, the target eccentricity manipulations most likely did not influence pre-saccade motor

preparation. Instead, a straightforward explanation may relate to the fact that the control condition was always completed prior to the proximal- and distal-weighting conditions. Such a finding represents a parsimonious account because pro- and antisaccades show practice-related improvements in RT (Dyckman & McDowell, 2005).

4.2. Prosaccade amplitudes are refractory to the manipulation of target frequency

Prosaccades undershot each target eccentricity and the magnitude of the bias was independent of the different weighting-conditions. The undershooting bias counters the range effect hypothesis' assertion that saccades to the 'proximal' and 'distal' targets within a stimulus-set respectively over- and undershoot *veridical target location* (Poulton, 1981; see also Kapoula, 1985). Instead, results support an extensive literature indicating that undershooting is an invariant control strategy that minimizes energy expenditure (Becker, 1989) and/or saccade flight time (Harris, 1995). Moreover, correlation coefficients showed that prosaccade RTs were neither consistently nor reliably related to amplitudes across each target eccentricity and weighting condition combination. Thus, the undershooting bias cannot be attributed to a speed/accuracy trade-off in movement planning (c.f. Abrams, Meyer, & Kornblum, 1989; Gillen & Heath, in press; Gillen, Weiler, & Heath, 2013; but see Kowler & Blaser, 1995). Additionally, that the undershooting bias was equivalent across the control, proximal- and distal-weighting conditions is consistent with the assertion that prosaccade sensorimotor transformations are mediated largely independent of top-down cortical processes via retinotopically organized motor maps in the superior colliculus (Wurtz & Albano, 1980). In other words, the top-down and context-dependent properties related to target frequency did not influence the absolute visual information mediating prosaccades.

4.3. Antisaccade amplitudes are characterized by perceptual averaging

Figs. 2 and 3 show that antisaccades undershot veridical target location and that the bias increased to a greater degree with target

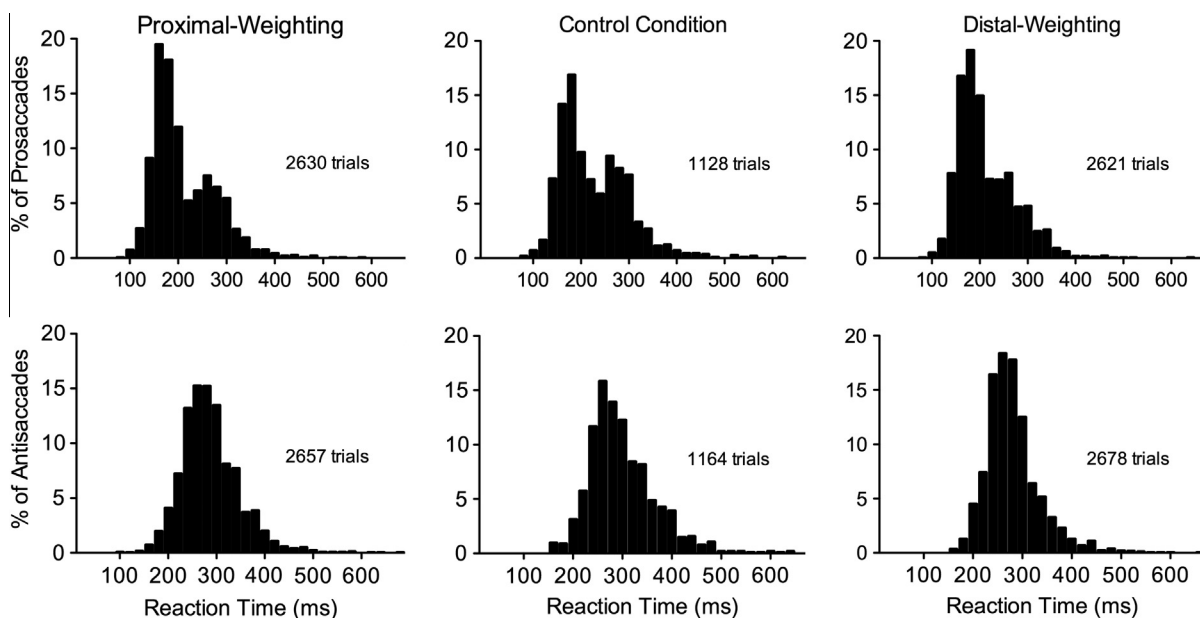


Fig. 5. Pro- (top panels) and antisaccade (bottom panels) reaction time (ms) distributions for proximal-weighting, control, and distal-weighting conditions. Bins represent 20 ms increments. Notably, the panels show that proximal- and distal-weighting conditions were not associated with an increased frequency of express saccades (i.e., a peak at approximately 100 ms: see Fischer & Ramsperger, 1984) relative to the control condition.

eccentricity than prosaccades (see also Dafoe, Armstrong, & Munoz, 2007; Evdokimidis, Tsekou, & Smyrnis, 2006; Gillen & Heath, in press) – a result countering the range effect hypothesis. As such, the current findings, as well as previous work (Amador, Schlag-Rey, & Schlag, 1998; Gillen & Heath, in press; Irving et al., 2009; Nyffeler et al., 2007), indicate that a general undershooting bias characterizes antisaccades.³ Moreover, the results for antisaccades are consistent with reports from the perceptual literature indicating that obligatory judgments (i.e., verbal reports) are increasingly underestimated as a function of target distance. For example, von Helmholtz's (1910/1962) seminal report showed that the perceived length of a peripherally presented line was inversely related to its eccentricity from a central fixation. Additionally, contemporary research has shown that perceptual judgments (Bingham & Pagano, 1998; Foley, 1980) and memory-based motor tasks (Heath, 2005; Knapp & Loomis, 2004; Sheth & Shimojo, 2001; Westwood, Heath, & Roy, 2003) exhibit a monotonic rise in underestimation/undershooting with increasing target distance. The increased bias is thought to reflect that the proportional increase in 'noise' associated with increasing stimulus magnitude (i.e., target eccentricity: for outline of Weber's law see: Marks & Algorn, 1998) engenders a compression of visual space toward a common and stable frame of reference (e.g., a central fixation cross). Importantly, the present results provide convergent evidence that the top-down nature of antisaccades results in response mediation via the same relative percept as that associated with visual perceptions.

The most salient finding from the present study was the modulation of the antisaccade undershooting bias across the different weighting conditions. Fig. 3 shows that the proximal- and distal-weighting conditions produced a respective increase and decrease in undershooting compared to the control condition. We believe that such a result supports the contention that perceptual averaging, in part, influences that visual percept supporting antisaccades. Recall that the perceptual averaging hypothesis asserts that the visual system represents target properties (e.g., size, luminance, distance) via an abstract approximation (i.e., the mean) of the individual targets included within a stimulus-set (Albrecht, Scholl, & Chun, 2012; Ariely, 2001; Chong and Treisman, 2003; Corbett & Oriet, 2011; Davarpanah Jazi & Heath, 2014). As indicated by Ariely, perceptual averaging allows the visual system to efficiently and effectively deal with limited attentional resources without simply reducing the resolution of individual target properties. Further, Treisman and Gormican (1988) reported that pre-attentive visual processes provide an average representation that is determined by the frequency that an individual feature (e.g., eccentricity) is presented within a visual set. Thus, and as demonstrated here (see also Gillen & Heath, in press), the presentation of target eccentricities with equal frequency resulted in the central target (i.e. the statistical summary) within the stimulus-set determining the direction and magnitude of the endpoint bias for the other targets in the set. In turn, the proximal- and distal-weighting conditions resulted in a statistical summary that was weighted in the direction of the most frequently presented target eccentricity. More directly, the visual percept supporting the proximal-weighting condition was governed by a statistical summary biased by the frequently presented 'proximal' target (i.e., 10.5°) – a bias that resulted in all targets within the stimulus-set eliciting more undershooting than the control condition. In turn, the increased frequency of the 'distal' target (20.5°) resulted in a percept

producing a decreased undershooting bias compared to the control condition.

A final issue that we address relates to the neural mechanism, or mechanisms, supporting perceptual averaging. Although we are unaware of neuroimaging or electrophysiological work examining this issue, perceptual averaging may be the result of independent or interdependent cortical and subcortical processes. A possible cortical explanation is that the neural populations associated with individual target eccentricities (Georgopoulos, Schwartz, & Kettner, 1986) are preshaped by partial information related to motor choices (Bastian, Schöner, & Riehle, 2003; Cisek, 2007). The preshaping is thought to allow the neural populations to encode a distribution of potential – as opposed to single – motor responses (Cisek & Kalaska, 2005). Thus, the top-down nature of antisaccades may result in the distributed peaks of neural activity related to different motor outcomes (i.e., the different target eccentricities) becoming partially aggregated into a single peak that represents the statistical summary of a stimulus-set. Although we are unclear as to the cortical region associated with this aggregation, the lateral intraparietal area (LIP) represents a candidate structure because it has been shown to serve the sensorimotor transformations underlying vector inversion (Zhang & Barash, 2000). In turn, a collicular-based explanation can be drawn from the prosaccade distractor literature. Indeed, a distractor presented proximal to a target results in a prosaccade amplitude that falls between the target and distractor (i.e., the global effect: see Coren & Hoenig, 1972; Findlay, 1982; Walker et al., 1997). Notably, electrophysiological evidence from non-human primates has linked the global effect to a spatial combination of visual and preparatory target and distractor signals within the visuomotor neurons of the superior colliculus (Dorris, Olivier, & Munoz, 2007). Thus, the top-down control of antisaccades may result in a low-level averaging of the relative target locations used in a stimulus-set.

5. Conclusions

The present results indicate that antisaccade sensorimotor transformations are supported via a relative visual percept. Moreover, our results show that the percept is governed, in part, via a statistical summary of the range of target eccentricities included in a stimulus-set (i.e., the perceptual averaging hypothesis).

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³ As indicated in the Introduction, target eccentricities less than ~6° have demonstrated an antisaccade overshooting bias. To our knowledge however, studies employing the range of eccentricities used here have consistently reported an antisaccade undershooting bias (Amador, Schlag-Rey, & Schlag, 1998; Evdokimidis, Tsekou, & Smyrnis, 2006; Gillen & Heath, in press; Irving et al., 2009; Nyffeler et al., 2007).

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