RESEARCH ARTICLE



The visual properties of proximal and remote distractors differentially influence reaching planning times: evidence from pro- and antipointing tasks

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Abstract The saccade literature has consistently reported that the presentation of a distractor remote to a target increases reaction time (i.e., the remote distractor effect: RDE). As well, some studies have shown that a proximal distractor facilitates saccade reaction time. The lateral inhibition hypothesis attributes the aforementioned findings to the inhibition/facilitation of target selection mechanisms operating in the intermediate layers of the superior colliculus (SC). Although the impact of remote and proximal distractors has been extensively examined in the saccade literature, a paucity of work has examined whether such findings generalize to reaching responses, and to our knowledge, no work has directly contrasted reaching RTs for remote and proximal distractors. To that end, the present investigation had participants complete reaches in target only trials (i.e., TO) and when distractors were presented at "remote" (i.e., the opposite visual field) and "proximal" (i.e., the same visual field) locations along the same horizontal meridian as the target. As well, participants reached to the target's veridical (i.e., propointing) and mirror-symmetrical (i.e., antipointing) location. The basis for contrasting pro- and antipointing was to determine whether the distractor's visual- or motor-related activity influence reaching RTs. Results demonstrated that remote and proximal distractors, respectively, increased and decreased reaching RTs and the effect was consistent for pro- and antipointing. Accordingly, results evince that the RDE and

the facilitatory effects of a proximal distractor are effector independent and provide behavioral support for the contention that the SC serves as a general target selection mechanism. As well, the comparable distractor-related effects for pro- and antipointing trials indicate that the visual properties of remote and proximal distractors respectively inhibit and facilitate target selection.

Keywords Antipointing · Distractor · Global effect · Propointing · Remote distractor effect

Introduction

Looking at and/or reaching to touch an icon on a computer tablet requires that the visuomotor system selects and defines the motor commands appropriate for the target icon while disregarding alternative actions afforded by nontarget (i.e., distractor) icons. Notably, the spatial relations between target and distractor influence the efficiency by which an appropriate movement plan can be selected. For example, Walker et al. (1997) reported that the simultaneous presentation of a target and a remote distractor (>20° in angular coordinates from the target axis) increased saccade reaction time (RT) compared to when a target was presented alone or when presented with a proximal distractor (i.e., within 20° of the ipsilateral target axis) (the remote distractor effect: RDE). In turn, distractor location elicits a converse effect on saccade endpoints. In particular, endpoints are biased in the direction of a proximal distractor but are refractory to a remote distractor (i.e., the global effect: Coren and Hoenig 1972; Deubel et al. 1984; Findlay 1982; Lévy-Schoen 1969; Walker et al. 1997).

In accounting for the RDE, Walker et al. (1997) proposed that competitive interaction between a "fixation



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system" and saccade-related activity in the superior colliculus (SC) influences saccade RTs (i.e., the fixation-system hypothesis). In particular, the hypothesis contends that a remote—but not proximal—distractor increases fixationsystem activity and inhibits/delays the evocation of a saccade via downstream projections to the brain stem (see also Findlay and Walker 1999). In contrast, lateral inhibition models (Godijn and Theeuwes 2002; Trappenberg et al. 2001) assert that the RDE arises from the transformation of target and distractor information within a common retinotopic map within the intermediate layers of the SC wherein discrete regions of activity (i.e., buildup neurons) related to each stimulus compete for a common movement threshold. As such, distractor-related activity at a distant location is predicted to inhibit saccade initiation via a long-range intercollicular inhibitory pathway (Takahashi et al. 2005). In turn, a proximal distractor results in target- and distractor-related buildup neuron activity that merges into a single peak and therefore hastens saccade RT (Corneil and Munoz 1996; Dorris et al. 2007). Thus, lateral inhibition models assert inhibitory and facilitatory effects of remote and proximal distractors, respectively. In terms of saccade endpoints and the previously mentioned global effect, fixation-system and lateral inhibition models assert that SC-related motor activity for a target and a proximal distractor merges into a single movement vector that represents a spatially average response rendering motor output biased in the direction of the distractor. In turn, both models assert that endpoints are refractory to remote distractors because target and distractor are represented via mutually exclusive peaks of SCrelated motor activity.

The first goal of the current investigation was to determine whether goal-directed reaches express a RDE and global effect similar to their saccade counterparts, and to determine whether proximal distractors influence reaching RTs. The basis for this question stems from non-human primate work showing that: (1) focal inactivation of the SC precludes the selection of a reaching target presented in the inactivated visual field (Song et al. 2011) and (2) singlecell recordings demonstrating that buildup neuron activity conveys target selection signals for reaching movements (Song and McPeek 2015). Accordingly, Song and McPeek proposed that the "... SC forms part of a general-purpose priority map that is used to guide a variety of goal-directed actions as well as covert attention" (p. 1420). In addressing our first research question, we are aware of one previous study examining expression of the RDE for reaching (McIntosh and Buonocore 2012). In that work, McIntosh and Buonocore specifically studied remote distractors (i.e., proximal distractors were not examined) presented 5° and 10° in the visual field opposite to a target and found that RTs in such conditions were no different than when compared to a target only condition. The authors therefore

concluded that the RDE represents a saccade-specific phenomenon. It is, however, important to recognize that McIntosh and Buonocore used a blocked target location paradigm such that within a block of 70 trials the target appeared either left or right of a central fixation. As such, participants were provided advanced information related to the location of both the target and the distractor—a manipulation that may have reduced online response planning and negated distractor-related planning effects (Khan et al. 2002; see also DeSimone et al. 2015). As such, we investigated distractor-related effects on goal-directed reaches wherein target and distractor (i.e., proximal and remote) locations could not be predicted in advance of their onset; that is, target and distractor locations were varied on a trialby-trial basis. In particular, participants completed reaches in a target only condition and when a target was presented simultaneous with a "proximal" or "remote" distractor (Fig. 1). Indeed, the inclusion of both proximal and remote distractors provides a direct framework for evaluating the theoretical tenets of fixation-system and lateral inhibition hypotheses.

The second goal of this study was to examine whether the sensory- (i.e., visual) or motor-related spatial relations between target and distractor influence reaching RTs and endpoints. The basis for this question stems from the fact that buildup neuron activity within the SC can reflect the visual- or motor-related properties of a to-be-completed response (Munoz and Wurtz 1995; Wurtz and Albano 1980). As such, we contrasted reaching responses directed to a target's veridical (i.e., propointing) and mirror-symmetrical (i.e., antipointing) location (see Heath et al. 2009a, b, 2012; Maraj and Heath 2010). To better underscore the basis for including antipointing trials, Fig. 2 demonstrates that for antipointing the visual properties of a proximal distractor (see Fig. 2a) are in the same visual field as the target (i.e., the distractor is visually proximal to the target); however, the movement's goal location is mirror-symmetrical and as such the motor-related properties of the response are remote to the distractor (see Fig. 2b). In turn, the bottom panels of Fig. 2 show that a remote distractor elicits the converse relationship; that is, the visual- (Fig. 2c) and motor-related (Fig. 2d) properties of the distractor are, respectively, remote and proximal to the target. In terms of research predictions, if a visual explanation accounts for distractor-related effects in goal-directed reaching then proand antipointing should demonstrate the RDE (and possible facilitatory effect of proximal distractors) and also show a global effect commensurate with saccades (Coren and Hoenig 1972; DeSimone et al. 2015; Findlay 1982; Walker et al. 1997). In turn, if the motor-related properties account for distractor effects then propointing should demonstrate a classic RDE and global effect, whereas antipointing responses should demonstrate longer RTs for a proximal



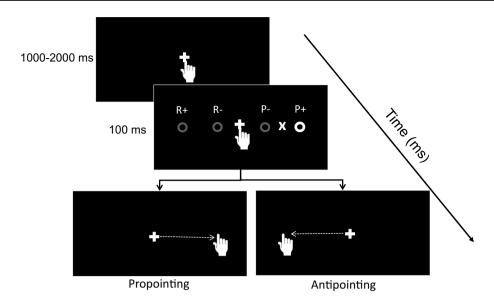


Fig. 1 Timeline of visual events. For simplicity, all stimuli are rendered as *white* instead of the color scheme described below. A centrally located green (i.e., propointing) or red (i.e., antipointing) fixation cross ("+") was presented for a 1000–2000 ms random foreperiod. Following the foreperiod, a yellow target ("×") was presented at a proximal (i.e., 190 mm) or a distal (i.e., 230 mm) location *left* or *right* of the fixation. For 20 % of the trials, the target was presented without a distractor (i.e., target only condition: TO). For 80 % of the trials, a yellow distractor stimulus ("o") was presented concurrently with the target in: (1) the same visual field as the distractor (i.e.,

proximal distractor: P) or (2) the visual field opposite to the distractor (i.e., remote distractor: R). The valence of a proximal distractor indicates whether it was presented at an eccentricity less than (i.e., P-) or greater than (P+) veridical target location, whereas the valence of a remote distractor indicates whether it was presented at an eccentricity less than (R-) or greater than (R+) the mirror-symmetrical target location. For this figure, we depict a single target eccentricity in the *right* visual field with a P+ distractor (the other distractor locations are depicted as light gray). The *last panel* in the timeline shows the instructed location of pro- (*left*) and antipointing (*right*) responses

distractor and endpoints that are biased in the direction of a remote distractor.

Methods

Participants

Twelve individuals (3 male and 9 female; age range 18–23 years) from the University of Western Ontario community volunteered for this experiment. All participants were self-declared right-hand dominant, had or normal or corrected-to-normal vision and had no self-reported history of neurological disease. Participants signed consent forms approved by the Office of Research Ethics, the University of Western Ontario, and this work was conducted according to the ethical standards outlined in the Declaration of Helsinki.

Apparatus and procedure

The apparatus consisted of a rectangular frame containing three shelves (for schematic, see Heath et al. 2009b). The top shelf supported a 30" computer monitor (60 Hz, 8-ms response rate, 1280 by 960; Dell 3007WFP, Round Rock,

TX, USA) that was used to project visual stimuli onto a one-way mirror (i.e., the middle shelf). The lower shelf was a solid surface (960 mm wide by 650 mm deep) and was the area where participants completed reaching movements. The distance between the top shelf and the middle shelf, and the middle shelf and the bottom shelf was constant at 340 mm. The optical geometry of the apparatus created a situation wherein participants perceived visual stimuli projected onto the mirror as being located on the lower shelf of the apparatus. A constant optical geometry was maintained via a head/chin rest (ASL-6000: Bedford, MA, USA), and all visual events were controlled via MATLAB (Version 7.9.0; The Math Works, Inc., Natick, MA, USA) and the Psychophysics Toolbox extensions (Version 3.0; Brainard 1997). The lights in the experimental suite were darkened throughout data collection, and in combination with the one-way mirror, vision of the reaching limb was occluded. As such, a splint complex containing dual lightemitting diodes (LEDs) was attached to the right index finger (i.e., the pointing finger) to provide a proxy for limb vision in order to affect: (1) a premovement sensorimotor calibration (Prablanc et al. 1979) and (2) online trajectory amendments. Notably, two previous studies by our group have directly shown that the LEDs serve as a reliable proxy for veridical limb vision (Heath 2005; Heath et al. 2004).



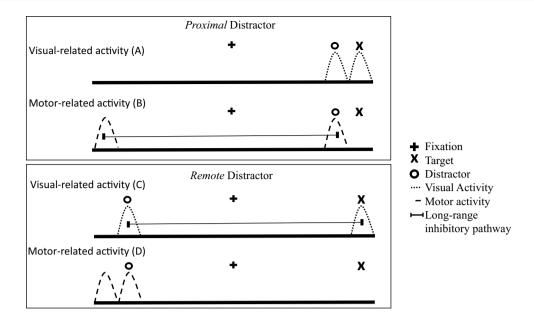


Fig. 2 Schematic for antipointing trials involving proximal (top panel) and remote (bottom panel) distractors. Proximal distractor: In the top panel, the row-labeled "Visual-related activity" (A) demonstrates that for antipointing (and also for a propointing trial) the visual activity of the distractor is "proximal" (i.e., in the same visual field) to the target. In contrast, the row-labeled "Motor-related activity" (B) demonstrates that the motor activity of the distractor is remote to the antipointing movement location (i.e., the response is in the opposite visual field). Remote distractor: For the bottom panel,

the row-labeled "Visual-related activity" (C) demonstrates that for antipointing (and also for a propointing trial) the visual activity of the distractor is "remote" (i.e., in the opposite visual field) to the target. Notably, if the visual property of the distractor influences antipointing (and propointing) then RTs should be increased due to a long-range intercollicular inhibitory pathway (i.e., the horizontal capped line). In turn, the row-labeled "Motor-related activity" (D) shows that antipointing motor activity of target and distractor are proximal (i.e., in the same visual field)

Participants sat for the duration of the experiment and used their right index finger to complete pro- (i.e., reach to the target stimulus) and antipointing (i.e., reach mirrorsymmetrical to the target stimulus) movements to visual targets. Visual stimuli included a green (i.e., propointing) and a red (i.e., antipointing) fixation cross (10 mm by 10 mm: ~1.1° by 1.1°) centered horizontally on the reaching surface and 230 mm from the surface's front edge. Yellow crosses (10 mm by 10 mm: ~1.1° by 1.1°) served as target stimuli and were located 190 mm (i.e., proximal target: ~20.8°) and 230 mm (i.e., distal target: ~24.7°) left and right of the fixation cross. Additionally, unfilled yellow circles (10 mm diameter: ~1.1°) served as task-irrelevant distractors. As shown in Fig. 1, distractors were located in the visual field ipsilateral (i.e., proximal distractor) and contralateral (i.e., remote distractor) to the target stimulus. Proximal distractors appeared at eccentricities that were 65 mm (~7.4°) less than (i.e., P-) and greater than (i.e., P+) the veridical target location, whereas remote distractors appeared at eccentricities that were 65 mm less than (i.e., R-) and greater than (i.e., R+) the target's mirror-symmetrical target location. We used the different target (i.e., proximal and distal) and distractor ("-" and "+") eccentricities to limit stereotyped trajectories from trial-to-trial in order to maximize online planning and control processes for any given trial.

For 20 % of trials, only the target was presented (i.e., target only condition: TO), whereas 80 % of trials were completed wherein a target was simultaneously presented with a distractor at proximal (i.e., P- and P+) or remote (i.e., R- and R+) locations.

In advance of each trial, participants used their right index finger to depress a start location microswitch that was superimposed over the fixation cross. Once the microswitch was depressed, a 1000-2000 ms foreperiod was initiated during which time the fixation remained visible. At the end of the foreperiod, a target (TO trials), or target with distractor (P-, P+, R- and R+ trials), was presented for 100 ms. The onset of the target (and distractor) served as the imperative to pro- or antipoint "as quickly and accurately as possible" and to ignore the irrelevant distractor when present. The fixation remained present throughout a trial (i.e., overlap paradigm) and participants were instructed to maintain their gaze at this location. To ensure fixation, the gaze location of participants left eye was recorded via a video-based eye-tracking system (Eye-Trac6: Applied Sciences Laboratory, Bedford, MA). Less than 5 % of trials for any participant involved a saccade or smooth pursuit eye movement (see Weiler et al. 2015), and such trials were discarded and re-entered into the random trial sequence. In addition, we note that if the target had remained visible throughout



a response then the direct stimulus—response mapping for propointing trials would have permitted feedback related to endpoint accuracy and therefore supported online control and offline learning (see Heath et al. 2009a, b; Maraj and Heath 2010; see also Khan et al. 2002). Of course, no such feedback would have been possible for antipointing trials because the required response was mirror-symmetrical to the target location. As such, the brief target presentation used here served to equate pro- and antipointing trials for the absence of on- and offline visual feedback.

Participants completed separate blocks of pro- and antipointing trials, and each block consisted of 200 trials (i.e., 400 total experimental trials). The ordering of pro- and antipointing blocks was counterbalanced across participants. Trial-type (TO, P-, P+, R-, R+), target eccentricity (i.e., proximal and distal) and visual field (left and right) were randomized within each trial block and presented on ten occasions for each experimental condition.

Data collection

In addition to containing LEDs, the splint complex affixed to the pointing finger contained an infrared-emitting diode (IRED). IRED position data were sampled at 400 Hz for 1000 ms following target onset via an OPTOTRAK Certus (Northern Digital Inc., Waterloo, ON, Canada). Offline IRED position data were filtered via a second-order dualpass Butterworth filter employing a low-pass cutoff frequency of 15 Hz. Filtered displacement data were used to compute instantaneous velocities via a five-point central finite difference algorithm. Movement onset was determined by an analogue signal driven by the release of pressure from the home position microswitch, whereas movement offset was determined as the first frame wherein resultant limb velocity fell below 50 mm/s for 20 consecutive frames (i.e., 50 ms).

Dependent variables and statistical analysis

We examined reaction time (RT: time from target onset to movement onset) and constant and variable error in the primary (i.e., horizontal) movement direction (negative and positive valences representing under- and overshooting bias, respectively). In particular, constant error was used to address putative global effects in pro- and antipointing. Trials involving directional errors (i.e., completing a propointing response instead of an instructed antipointing response and vice versa) were not included in subsequent data analyses (DeSimone et al. 2014) and pro- and antipointing trials entailed 1 and 6 % directional errors, respectively (cf. Heath et al. 2009a; Maraj and Heath 2010). The low error rates are expected and are attributed to the use of an overlap paradigm and the completion of pro- and antipointing trials

in separate blocks (Heath et al. 2011; Olk and Kingstone 2003). Furthermore, for each participant, an average of 4 % of trials were omitted from data analyses due to: (1) IRED signal loss during the reaching response, (2) an anticipatory response (i.e., RT < 100 ms) (see Maraj and Heath 2010) and (3) RT or constant error more than 2.5 standard deviations above a participant-specific mean.

In most cases (see exceptions below), data were examined via 2 (task: pro- and antipointing) by 5 (trial-type: TO, P-, P+, R- and R+) by 2 (target eccentricity: proximal and distal) ANOVAs. An alpha level of 0.05 was set for all statistical comparisons, and main effects and interactions involving distractor condition were decomposed via planned comparisons between each distractor condition (i.e., P-, P+, R- and R+) and the TO condition. In particular, main effects/interactions involving distractor condition were decomposed via graphical comparisons of point (i.e., mean distractor difference score: distractor condition [P-/P+/R-/R+] minus TO condition) and interval (i.e., 95 % confidence interval) estimates (Cumming 2013). To demonstrate our graphical technique, the smaller offset panels of Fig. 3 show mean participant-specific RT distractor difference scores and associated 95 % confidence intervals separately for pro- and antipointing. Importantly, the absence of overlap between a confidence interval and zero (i.e., the horizontal lines) demonstrates that a distractor condition reliably differed from the TO condition, and the valence of the score indicates the direction of the RT change. For example, the negative difference scores associated with proximal distractors (i.e., P- and P+ trials) indicate a distractor-related RT "savings." In contrast, the positive difference scores for remote distractors (i.e., R- and R+ trials) indicate a distractor-related RT "cost." Further,

¹ The visual field associated with target presentation did not reliably influence RTs for the different conditions (F < 1) or produce a higherorder interaction with distractor condition (all F < 1.5). Results for CE indicated a task by visual field interaction, F(1,11) = 12.96, p < 0.04, $\eta_p^2 = 0.54$, such that antipointing responses in the left visual field (-42.5 mm, SD = 28.1) exhibited a large magnitude undershooting bias and right visual field responses (13.1, SD = 28.1)exhibited an overshooting bias. In turn, the magnitude of the underand overshooting bias for left (-16.1 mm, SD = 14.3) and right (13.0, SD = 14.5) propointing responses was less (for review of this issue see Heath et al. 2009a, b; Maraj and Heath 2010). Most notably, the inclusion of visual field in our ANOVA model for CE did not elicit any higher-order interactions with distractor condition (all F < 1). For that reason, we did not include visual field (i.e., target presented left or right of fixation) in the ANOVA model presented in the Results. Moreover, although McIntosh and Buonocore's (2012) RT findings indicated a three-way interaction involving target eccentricity by distractor location by visual field the authors stated: "There was insufficient statistical power to support a formal investigation of this interaction..." (p. 204). Thus, convergent evidence indicates that the visual field associated with target presentation does not reliably modulate a RDE or global effect in pro- or antipointing.



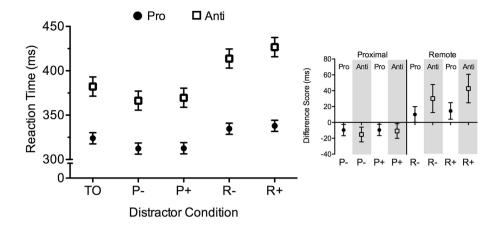


Fig. 3 Main panel presents mean reaction time (ms) for pro- and antipointing trials as a function of target only (TO) and proximal (P- and P+) and remote (R- and R+) distractor conditions. *Error bars* in the main panel represent 95 % within-participant confidence intervals as a function of the mean-squared error term for distractor condition computed separately for pro- and antipointing (Loftus and Masson 1994). The offset panel shows distractor condition difference scores (P-/P+/R-/R+ minus TO) for pro- (*closed circle symbols*) and antipointing (*open square symbols*). *Error bars* represent the 95 % between-participant confidence intervals. The absence of

overlap between an *error bar* and zero represent a reliable difference between a given distractor condition and its matched TO condition, and such a finding can be interpreted inclusive to a test of the null hypothesis. In turn, an *error bar* that overlaps with zero indicates that the given distractor condition and its matched TO condition do not reliably differ. *Note*: visual inspection of propointing R— trials suggests that the *error bar* overlaps with zero; however, there is not direct overlap and such a finding indicates that the condition reliably differs from zero (Cumming 2013)

and although not demonstrated in Fig. 3, overlap between a difference score and zero indicates a null difference between a distractor condition and its TO condition counterpart. According to Cumming, the benefit of this approach is that it provides point and interval estimates in units that are meaningful to the experimental context and are directly linked to p values.

Results

Results for RT yielded a main effect for target eccentricity, F(1,11) = 8.08, p < 0.02, $\eta_p^2 = 0.42$, indicating that values were shorter for the distal (355 ms, SD = 57) than the proximal (364 ms, SD = 59) target. In addition, RT yielded main effects for task, F(1,11) = 64.93, p < 0.001, $\eta_{\rm p}^2=0.85$, trial-type, $F(4,44)=33.92,\,p<0.001,\,\eta_{\rm p}^2=0.75$ and their interaction, $F(4,44)=9.17,\,p<0.001,\,\eta_{\rm p}^2=0.45.$ As shown in Fig. 3, propointing RTs were always less than antipointing. Moreover, the offset panel of Fig. 3 shows that pro- and antipointing RTs for proximal (P- and P+) and remote (R- and R+) distractors were, respectively, shorter and longer than their TO trial counterparts. Thus, our post hoc decomposition did not uncover the nature of the task by distractor condition interaction. Accordingly, for each participant, we computed distractor condition difference scores (i.e., distractor condition [P-, P+, R-, R+] minus TO condition) to examine whether distractor-related planning effects differed in magnitude between pro- and

antipointing. Difference scores were examined via 2 (task: pro- and antipointing) by 4 (trial-type: P-, P+, R- and R+) repeated measures ANOVA and results revealed a main effect for trial-type, F(3,33) = 40.64, p < 0.001, $\eta_p^2 = 0.78$, and a task by trial-type interaction, F(3,33) = 10.43, p < 0.001, $\eta_p^2 = 0.49$. In decomposing the interaction, we first completed within-task contrasts to determine if distractor effects varied with distractor eccentricity (i.e., P- vs. P+ and R- vs. R+ separately for pro- and antipointing). Results showed that difference scores did not reliably vary for propointing trials involving proximal or remote distractors or antipointing trials involving proximal distractors [all t(11) = -0.65, -1.40 and -1.16, ps = 0.95, 0.18 and 0.27]. In contrast, the offset panel of Fig. 3 shows that antipointing trials in the R+ condition produced a larger difference score than its R- counterpart [t(11) = -3.68, p < 0.01]. A second series of contrasts entailed between-task comparisons; that is, we contrasted difference scores for pro- and antipointing at matching distractor locations. For proximal distractors, pro- and antipointing difference scores did not reliably differ [all t(11) = 1.39 and 0.25, respectively, for P- and P+ trials, ps = 0.19 and 0.80]; however, for remote distractors, antipointing trials produced larger difference scores than their propointing counterparts [all t(11) = -2.37 and -3.55, respectively, for R- and R+ trials, ps < 0.04 and 0.01]. In other words, the RT "savings" afforded by proximal distractors was similar across pro- and antipointing, whereas the RT "cost" for remote distractors was larger for antipointing.



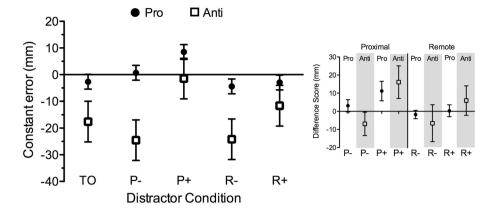


Fig. 4 Main panel presents mean constant error (mm) for pro- and antipointing trials as a function of target only (TO) and proximal (P- and P+) and remote (R- and R+) distractor conditions. The *offset panel* shows distractor condition difference scores (P-/P+/R-/R+

minus TO) pro- (closed circle symbols) and antipointing (open square symbols). Error bars and interpretation of the offset panel as per the conventions outlined in Fig. 3

yielded main effects Constant error of F(1,11) = 16.41, p < 0.01, $\eta_p^2 = 0.60$, target eccentricity, F(1,11) = 184.79, p < 0.001, $\eta_p^2 = 0.94$, trial-type, F(4,44) = 12.96, p < 0.001, $\eta_p^2 = 0.54$, and interactions involving task by target eccentricity, F(1,11) = 40.42, p < 0.001, $\eta_p^2 = 0.78$, and task by trial-type, F(4,44) = 5.70, p < 0.01, $\eta_p^2 = 0.34$. The task by target eccentricity interaction indicated that propointing responses to the proximal (3.8 mm, SD = 13.5) and distal (-5.0 mm, SD = 12.3) targets, respectively, over- and undershot veridical target location [t(11) = 7.71, p < 0.001]. In turn, antipointing responses undershot proximal (-4.6 mm, SD = 22.5) and distal (-25.9 mm, SD = 22.9) targets with the undershooting bias increasing with target eccentricity [t(11) = 12.16, p < 0.001]. Figure 4 shows the task by distractor condition interaction. For propointing, P+ trials overshot their TO trial counterpart; however, P- trials and remote distractors (i.e., R- and R+ trials) did not reliably differ from TO trials. For antipointing, P and P+ trials, respectively, exhibited an under- and overshooting bias compared to TO trials. In turn, remote distractors (i.e., R— and R+ trials) and TO trials did not reliably differ.

Variable error yielded main effects for task, F(1,11) = 26.04, p < 0.001, $\eta_p^2 = 0.70$, and trial-type, F(4,44) = 5.43, p < 0.01, $\eta_p^2 = 0.33$. As expected, propointing (22 mm, SD = 5) endpoints were less variable than antipointing (36 mm, SD = 12). In decomposing the trial-type main effect, we contrasted each distractor condition with the TO condition. Results indicated that P- (29.3 mm, SD = 8.2), R- (26.7 mm, SD = 2.5) and R+ (27.3 mm, SD = 2.3) trials did not reliably differ from the TO (28.7 mm, SD = 7.3) condition [all t(11) = 1.24, 1.11 and 0.67, respectively, for P+, R- and R+ trials, ps = 0.24, 0.28 and 0.51], whereas endpoints for P+ (32.7 mm, SD = 8.2) trials were more variable than TO trials t(11) = 5.34, p < 0.001.

Discussion

Propointing: proximal and remote distractors respectively decrease and increase RT

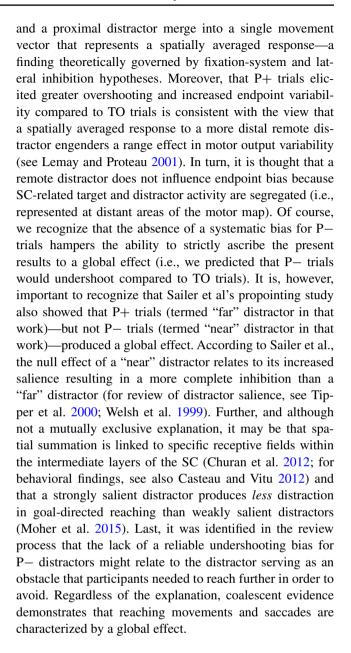
The first objective of this study was to examine the degree and direction that proximal and remote distractors influence RTs for reaches involving direct stimulus-response relations (i.e., propointing). Recall that McIntosh and Buonocore (2012) examined the effects of remote distractors on propointing RTs and reported that planning times were no different than target only (i.e., TO) trials—a result the authors interpreted as providing evidence that the remote distractor effect (RDE) is a saccade-specific phenomenon. Importantly, and as underscored in the Introduction, the target and distractor locations used by McIntosh and Buonocore were spatially predictable and may have therefore precluded any online selection necessary to disentangle target and distractor locations. As such, the present study randomly varied target and distractor location on a trial-by-trial basis. Given this approach, propointing RTs for remote distractor trials were longer than their TO trial counterparts, and the magnitude of the inhibitory effect was consistent for R- and R+ trials. Thus, the present results suggest that the online selection of a target from a nontarget is an important consideration in the elicitation of a propointing RDE, and results support Song and McPeek's (2015) assertion that the SC serves as an effector-independent target selection mechanism.

The RDE outlined in the preceding paragraph is consistent with the saccade literature and is predicted by fixation-system (Findlay and Walker 1999) and lateral inhibition (Trappenberg et al. 2001) hypotheses. The present study also included proximal distractors (i.e., P— and P+ trials)



to test the contrasting predictions that a proximal distractor produces a null (i.e., fixation-system hypothesis) or facilitatory (i.e., lateral inhibition hypothesis) RT effect. Results showed that proximal distractors produced shorter RTs than TO trials, and the magnitude of the facilitatory effect was consistent across P- and P+ trials. This result counters some evidence from the saccade literature (e.g., Deubel et al. 1984; Walker et al. 1997)—including work by our own group (DeSimone et al. 2015)—and does not support the fixation-system hypothesis (Findlay and Walker 1999). It is, however, important to recognize that other work in the saccade literature has reported that proximal distractors hasten RTs (Corneil and Munoz 1996; Dorris et al. 2007) and is a result supporting the lateral inhibition hypothesis' contention that a localized spread of excitatory activity within adjacent regions of the SC facilitates response planning (Godijn and Theeuwes 2002; Trappenberg et al. 2001). Put another way, the lateral inhibition hypothesis contends that proximal distractors enhance neural activity related to target selection. Thus, our results are compatible with the lateral inhibition hypothesis and provide some evidence that goal-directed reaches and saccades share a similar, and collicular-based, target selection mechanism. More specifically, our findings are consistent with Song et al's (2011) assertion that target selection signals in the SC do not simply represent competition among different eye-movements, but instead reflect an abstract and effector-independent priority map influencing target selection.

In addition to RT, we examined whether proximal and remote distractors differentially influenced propointing endpoints (i.e., constant and variable error). In addressing this issue, we are aware that McIntosh and Buonocore (2012) and Sailer et al. (2002), respectively, examined the influence of remote and proximal distractors on propointing endpoints. The former study reported that remote distractors did not systematically influence endpoints (i.e., constant and variable error), and the latter study indicated that endpoints were generally biased in the direction of a proximal distractor. Notably, and to our knowledge, no study has directly contrasted propointing endpoint bias across proximal and remote distractors. Our results showed that P+ trials exhibited an overshooting bias compared to TO trials, whereas P- and remote (R- and R+) distractors produced endpoints comparable to TO trials. The overshooting bias of P+ trials and the null effect for remote distractors are consistent with findings from the saccade literature (Coren and Hoenig 1972; DeSimone et al. 2015; Deubel et al. 1984; Lévy-Schoen 1969; Walker et al. 1997) and the individual remote and proximal distractor paradigms outlined in the aforementioned reaching studies (i.e., McIntosh and Buonocore 2012; Sailer et al. 2002). The saccade literature has attributed the overshooting bias of a proximal distractor to a "global effect" wherein SC activity related to a target



Antipointing: the visual properties of a distractor influence RT

The second objective of our study was to determine whether the visual- or motor-related properties of a distractor influence RT. To accomplish that objective, we included a condition wherein participants reached mirror-symmetrical to the location of a target (i.e., antipointing). As expected, antipointing RTs were longer than their propointing counterparts and it is a result that neuroimaging and electroencephalographic work has attributed to the top-down (i.e., cognitive) and time-consuming demands of: (1) inhibiting a stimulus-driven propointing response (i.e., response suppression) and (2) the visual remapping of a target's spatial properties in mirror-symmetrical space (i.e., vector



inversion) (Connolly et al. 2000; Heath et al. 2012, 2015; for review of antisaccades, see Munoz and Everling 2004). Notably, in spite of the increased antipointing processing demands, results showed that the pattern of distractorrelated planning effects was comparable to those associated with propointing. In particular, proximal and remote distractors respectively decreased and increased RTs, and the magnitude of the facilitatory effect for proximal distractors was independent of distractor eccentricity (i.e., P- trials = P+ trials). In fact, the only identified within-task difference in pro- and antipointing distractor-related RT effects was that the latter showed a larger RT planning cost with increasing distractor eccentricity (i.e., R+ trials > R- trials)—a finding that might relate to eccentricity related costs of disentangling target from distractor and subsequently computing a mirror-symmetrical response (Casteau and Vitu 2012).

The most notable feature of our comparison between pro- and antipointing trials is that they demonstrated matching facilitatory and inhibitory planning related effects for proximal and remote distractors, respectively. Indeed, and as shown in Fig. 2, if planning times were influenced by a distractor's motor-related activity then antipointing trials should have demonstrated RT effects converse to propointing (see Fig. 2b). Instead, the inhibitory effect of a remote distractor indicates that the visual-related activity of a distractor at a remote area in the collicular map inhibits response planning, whereas adjacent visual activity in the collicular map facilitates response planning. Support for our interpretation is bolstered by the fact that antipointing demonstrated the same general pattern of distractor-specific endpoint bias as propointing. Indeed, the only difference between pro- and antipointing endpoints was that P- trials in the latter task showed a reliable undershooting bias compared to their TO trial counterparts. In other words, antipointing trials demonstrated a global effect across Pand P+ trials and represents a finding that may, in part, relate to the fact that the top-down (i.e., perceptual) nature of antisaccades renders action output mediated via relative visual information (for review of this issue, see Heath et al. 2009a, b; Maraj and Heath 2010; Rossit et al. 2011). In addition, our "visual" interpretation is consistent with single-cell recording work in non-human primates showing that buildup neuron activity in the motor maps of the SC can selectively represent the visual properties of a stimulus (Munoz and Wurtz 1995; Wurtz and Albano 1980). Moreover, the combined results for pro- and antipointing trials are compatible with the lateral inhibition hypothesis and the view that the SC serves as a general target selection mechanism for dissociating the visual properties of target and nontarget stimuli.

A final issue that we address relates to the observation that antipointing trials performed with a remote distractor exhibited larger RT inhibitory effects than their propointing

counterparts, whereas the facilitatory effect for pro- and antipointing trials with a proximal distractor did not reliably vary. The larger RT inhibitory effect for antipointing may relate to the top-down and obligatory (i.e., cognitive) need to adopt the appropriate task rule for decoupling the spatial relations between stimulus and response (Sato and Schall 2003). Indeed, it may be that adoption of the appropriate antipointing task rule (i.e., a high-level selection process attributed to the dorsolateral prefrontal cortex: see Everling and Johnston 2013) in combination with longrange intercollicular inhibition accompanying the presentation of a remote distractor further impedes antipointing planning times. This is an issue that future work by our laboratory will explore via electroencephalographic examination of distractor effects in antipointing (e.g., Heath et al. 2012, 2015; Weiler et al. 2015). In particular, we seek to identify a putative event-related brain potential (i.e., the P300; for review, see Donchin and Coles 1988) related to the increased RT inhibitory effect for an antipointing response performed with a remote distractor.

Conclusions

Proximal and remote distractors respectively facilitated and inhibited pro- and antipointing RTs—a result consistent with the lateral inhibition hypothesis and providing corollary behavioral evidence that the SC serves as a general, and effector-independent, target selection mechanism. Moreover, we propose that the equivalent pro- and antipointing distractor-related RT effects observed here indicates that a distractor's visual properties influence the efficiency and effectiveness of target selection.

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