Identifying a Distractor Produces Object-Based Inhibition in an Allocentric Reference Frame for Saccade Planning

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Abstract:

We investigated whether distractor inhibition occurs relative to the target or fixation in a perceptual decision-making task using a purely saccadic response. During the process of discriminating a target from distractor, saccades made to a target deviate towards the distractor. Once discriminated, the distractor is inhibited, and trajectories deviate away from the distractor. Saccade deviation magnitudes provide a sensitive measure of target-distractor competition dependent on the distance between them. While saccades are planned in an egocentric reference frame (locations represented relative to fixation), object-based inhibition has been shown to occur in an allocentric reference frame (objects represented relative to each other independent of fixation). By varying the egocentric and allocentric distances of the target and distractor, we found that only egocentric distances contributed to saccade trajectories shifts towards the distractor during active decision-making. When the perceptual decision-making process was complete, and the distractor was inhibited, both ego- and allocentric distances independently contributed to saccade trajectory shifts away from the distractor. This is consistent with independent spatial and object-based inhibitory mechanisms. Therefore, we suggest that distractor inhibition is maintained in cortical visual areas with allocentric maps which then feeds into oculomotor areas for saccade planning.

Introduction

When I view a tabletop full of coffee cups, I can locate my cup relative to myself in a viewpoint-dependent, egocentric reference frame. When I want to reach for my cup, there is considerable evidence that both my eye- and hand-movements are programmed using an ego-centric spatial map of the scene. However, if I want to avoid knocking over my colleagues' cups, I need to direct my actions towards my cup while considering the locations of the non-target cups. This requires an allocentric (object-to-object) spatial map of the scene, where objects are represented in a viewpoint-independent reference frame. There is converging evidence from behavioral, electrophysiological, and imaging studies that we use both viewpoint-dependent egocentric, and viewpoint-independent allocentric reference frames in spatial cognitive tasks using reaching[1][2][3][4].

When there are multiple objects in the visual scene, attending to and acting on, relevant stimuli requires the suppression of irrelevant stimuli competing for attentional selection. Yet there is no clear delineation about the reference frames supporting this suppression. In models of attention based on visual processing for example, the biased competition and selective tuning models, the suppression of irrelevant stimuli changes in strength based on the proximity to an attended stimulus[5][6]. However, oculomotor models of spatial attention invoke regions encoding relevant and irrelevant object locations entirely in retinotopic coordinates[7][8][9].

Recently, saccadic eye movement trajectories have been shown to reflect the continuous competition resolution between objects[10]. Specifically, before the target object has been differentiated from a distractor, and decision making is still actively taking place, saccades deviate towards the distracting object. However, once the target and distractor are differentiated, and decision making has completed, the saccades deviate away from the distractor. Saccades are

planned in an egocentric reference frame on a retinotopic map of space[11] and activity on this map has been shown to cause saccade trajectory deviations[12][13]. The deviation towards a distractor is due to increased activity at the location of the distractor, whereas suppression at the distractor location leads to deviation away. Because saccade planning is egocentric[14][15][16], it is assumed that the suppression of distractors would also be egocentric.

However, behavioral studies in humans have shown that object-based suppression can also occur in allocentric reference frames. For example, object-based inhibition of return (IOR) has been shown to occur in an allocentric reference frame[17][18][19][20]. Both trajectory deviations and IOR can occur under the same conditions but do so on different timescales[21]. The complex objects used by Giuricich, and colleagues[10] required late-stage visual processing to discriminate target from distractor[22][23]. These late-stage ventral stream areas (e.g. TE, TEO, IT cortex) support object representations in allocentric reference frames[24], likely resulting from large, bilateral receptive fields with position and size invariance[25][26]. So, if saccade planning occurs in an egocentric reference frame, but the resolution of object competition is dependent on regions with allocentric representations and both involve inhibition of a distractor, what is the reference frame of the resulting distractor suppression?

In this study we independently varied the egocentric and allocentric distance of a target and distractor to investigate the reference frame of distractor suppression. The egocentric distance of the target and distractor is their eccentricity, while the allocentric distance describes the distance between the target and distractor or target-distractor distance (T-D distance), which is independent of the viewpoint or eye position. Varying the eccentricity of the target and distractor while keeping the angle between them constant, leads to a range of T-D distances. Using saccade trajectories to infer the state of decision-making, we identified when the distractor has been

suppressed through the resulting deviation away from the distractor. The magnitude of the saccade deviation is associated with the strength of the distractor-related-activity, meaning the amount of deviation at different egocentric and allocentric distances will reflect the reference frame of distractor suppression. As the oculomotor system encodes saccades to a target in an egocentric reference frame, we expect to find egocentric reference frame effects on saccade trajectories both during active competition before the decision is made and after, when the distractor is suppressed. However, if distractor suppression is dependent on object-based inhibition developing in cortical visual areas, once the competition is resolved, saccade trajectories should also be shifted based on T-D distance in an allocentric reference frame.

Methods

Participants

Forty naïve participants (8 males; age: 18-27, mean = 19.6 years old) were recruited for the current experiment. All participants had normal or corrected to normal vision, gave written informed consent, and were compensated with $15 CAD for their time. Ethics approval of the experiment was obtained from the Research Ethics Board at the University of Guelph.

Stimuli and Apparatus

Participants were seated in a dimly lit room 57cm away from a 21” CRT monitor (60Hz, 1024×768), with movement reduced by use of a chin and head rest. Stimulus presentation and data collection was controlled by Presentation software (Neurobehavioral Systems, Inc., Berkeley, CA), and participant responses were made using a response box (RB-540, Cedrus Corp., San Pedro, CA) and eye movements. The eye movements of participants were recorded from their right eye using an Eyelink II infrared eye tracker (500Hz; SR Research, ON, Canada).

The target and distractor stimuli were white (CIExy = [.29, 0.30]; luminance = 126.02cd/m^2) on a black (CIExy = [.27, 0.26]; luminance = 0.20cd/m^2) background and were randomly selected from a set previously used[27] (Fig. 1a). Each stimulus consisted of 6- or 7-line segments (1° × 0.08°). The number of line segments and the limitations of human visual working memory capacity required that the objects are represented as singular complex objects.

Procedure

Participants completed a delayed match to sample task, making saccades to a previously shown target presented with a distractor (Fig. 1c). Eye position was calibrated at the beginning of the experiment, at the start of each block, and additionally if necessary. Each trial began with a fixation cross (0.4° X 0.4°; CIExy = [.x=29, y=0.30]; 126.02cd/m^2) at the center of the screen. Following 200 ms fixation, the target object was presented at the centre of the display and remained until the participant pressed a designated button on a response box. The target object was replaced by a fixation cross and the participant had to maintain fixation for 200 ms or the trial was terminated. The fixation marker remained on the display while the target and a distractor object appeared simultaneously for 750 ms or until the participant made a saccade to one of the objects. Participants received a written error message and audible tone if they failed to make a saccade or made a saccade to the distractor object; error trials were presented later in within the same block.

There were 15 potential positions for the objects, organized into 5 different branches separated by 45°, and placed at egocentric eccentricities of 7, 10, or 13 dva (Fig. 1b). The various eccentricities for the target and distractor yield a range of allocentric distances between them (T-D distance), ranging from 5.36 dva to 9.95 dva. Once the target position had been determined for a given trial, the distractor was placed on an adjacent branch at one of the 3 eccentricities.

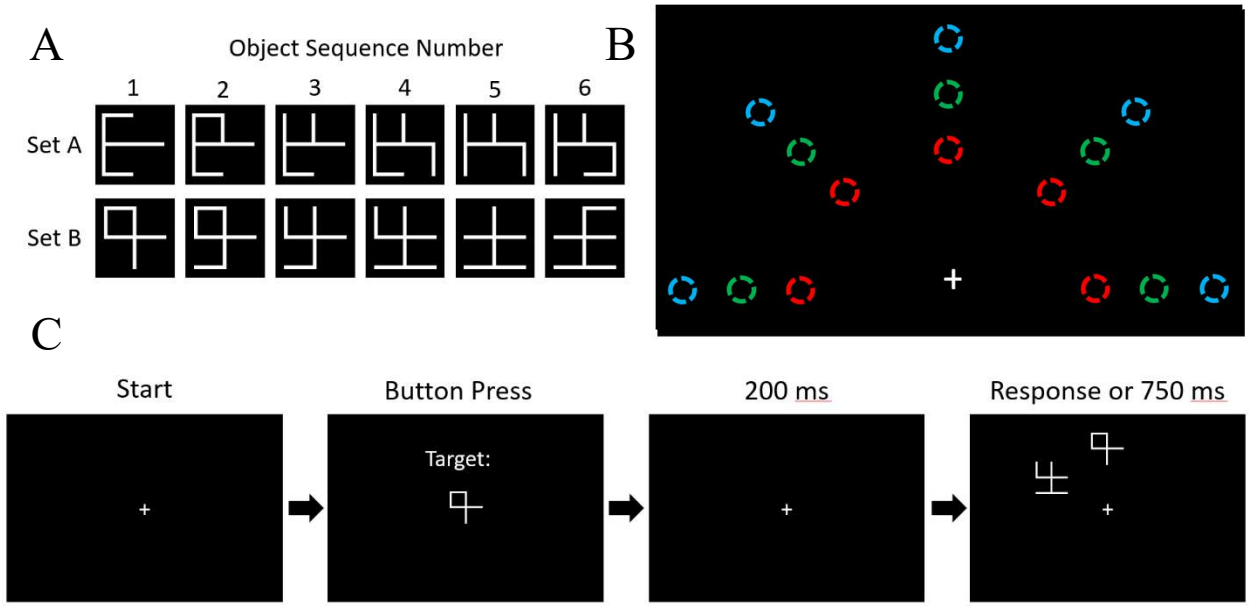


Figure 1: Experimental Overview A) The stimuli were selected from 2 sets of 6 objects, each 2° X 2°. The target and distractor on a trial were drawn from the same set, with each object varying by one line addition or removal, relative to adjacently numbered objects in the set. The objects were designed to avoid resemblance to any English characters or numbers to ensure their novelty to participants. B) The objects were presented at 15 possible locations at 3 eccentricities (depicted in color for clarity in the figure only: 7 [red], 10 [green], and 13 [blue] dva from fixation), and 5 branches separated by 45° in the upper half of the display. The target and distractor were always objects from the same set and presented along adjacent branches. C) Trials began with participants fixating a central cross, which was replaced with a preview of the target for that trial. After participants pressed a button, they were required to again fixate a cross for 200ms before the target and distractor appeared simultaneously. The objects remained on screen until either a saccade was made to the target or distractor or 750ms had elapsed. Trials without a response in 750ms were presented again at a later point in the block, and there were some trials where only the target was presented to establish a saccade baseline.

Objects only appeared on or above the horizontal meridian, leading to 72 target-distractor position combinations (Fig. 1b). Additionally, each block contained target-only trials at each of the 15 object positions, acting as a baseline, producing a total block size of 87 trials. Each participant completed 5 experimental blocks (435 total trials) and a 10-trial practice block presented at the beginning of the experiment that was not included in analysis.

Data Analysis

Saccade Detection: Saccades were detected using in-house MATLAB (Mathworks, Natick, MA) scripts following pre-determined criteria; an eye movement with a velocity greater than 20°/s for at least 8 ms with a peak velocity greater than 50°/s. Saccades were evaluated manually to remove trials where the first saccade was not made to the target or distractor (9.59%). Trials with short (amplitude < 1° [0.65%]) or express saccades (Saccade Reaction Time (SRT) < 100 ms [1.97%]) or where no eye position data was recorded (3.64%) were excluded from further analysis. Overall, 84.15% of recorded trials were included for analysis.

Accuracy: Accuracy was calculated for each participant as the proportion of trials that a saccade was made to the target rather than the distractor. All participants' performance exceeded chance (binomial distribution with $p = 0.5$ [50%]).

Saccade Trajectory Metrics: To quantify the deviation of a saccade from a straight path, the sum curvature and endpoint angle for each saccade was calculated. The sum curvature provides a measure of the strength of target and distractor representations in the cortical saccade planning process[28]. Sum curvature was calculated as the total deviation of a saccade from a straight line between its start point and endpoint (reference line). The endpoint angle of a saccade is suggested to result from the outcome of a subcortical vector average of saccade plans to both the target and distractor[29][30]. The endpoint angle was calculated as the polar angle (in degrees)

between the reference line and a straight path from the saccade start point to the center of the target. Both metrics were normalized by subtracting the mean values from target only trials and corrected such that positive values reflect deviations towards the distractor and negative values reflect deviations away from the distractor.

Processing Time Division: Following Giuricich and colleagues[10], trajectory metrics were used to separate saccadic responses made between active and completed decision making stages. The short processing time range was determined by saccade latencies with significant deviations towards the distractor, while the long processing time range was determined by saccade latencies with significant deviations away from the distractor.

Results

The short processing time range was determined to be 100ms – 196ms for both performance (accuracy) and eye movement (sum curvature and endpoint angle) metrics. The long processing time was found to be 250ms – 750ms for accuracy and sum curvature, and the slightly later 280ms - 750ms period for the endpoint angle metric. Saccades with SRTs between the short and long processing time ranges contain a mixture of saccades with curvatures towards and away from the distractor and were excluded from further analysis.

Accuracy

Increasing the distance between fixation and the stimuli (egocentric reference frame) would be expected to reduce accuracy. To investigate the relationship between an egocentric reference frame and accuracy over processing times, a multiple linear regression with target and distractor eccentricity, and processing time (short and long) as factors was performed. The overall regression was found to be highly significant ($R^2 = 0.641$, $F(7,680) = 173.2$, $p < 2.2X10^{-16}$).

Increasing target eccentricity was found to decrease accuracy, while increasing distractor eccentricity increased accuracy (Figure 2). The effect of both target and distractor eccentricity significantly decreased from short to long processing time. There was a significant interaction between target and distractor eccentricity that did not change with processing time, suggesting a relationship between object positions beyond their individual eccentricities, that will be explored in the next section. Finally, there was no change in accuracy across processing times independent from the other relationships mentioned above. However, a Wilcoxon signed rank test across each participant and object eccentricity condition revealed a significant increase in accuracy at longer processing times (all p's < 0.0001).

To identify any effects of an allocentric reference frame on accuracy, a multiple linear regression with processing time and target-distractor distance (T-D distance) was performed on the subset of trials in which the target eccentricity and distractor eccentricity were equal, i.e. equal egocentric distances (Table 1). The regression across T-D distance was significant overall, and robust across participants (R^2: 0.332, $F(3,224) = 37.14$, $p < 2.2X10^{-16}$). While overall accuracy increased significantly from short to long processing time ($p = 0.0156$), T-D distance had no influence on accuracy at short processing times. Critically, accuracy varied by T-D distance at long processing times, when the distractor is inhibited, decreasing significantly as the T-D distance increased.

We also compared conditions where the T-D distance between the target and distractor was identical, but their eccentricities varied to differentiate between egocentric and allocentric encoding. Using pairwise t-tests (Figure 3), at long processing times, we see evidence of an allocentric effect, as well as significant differences between eccentricities (all $p < 0.01968$).

Taken together, these results indicate that at long processing times accuracy is driven by object distance in both egocentric and allocentric reference frames.

Table 1: Regression Coefficients, t-values, and p-values for Accuracy and Trajectory Metrics Over Processing Time. *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$, n.s.: not significant. Note: the values reported for accuracy regressions were determined through separate linear regressions for short and long processing time after differences had been established. ŧ is used to indicate coefficients that were not significantly different between processing times.

	Regression Predictor	Accuracy	Sum Curvature	Endpoint Angle
Short Processing Time	Target Eccentricity	-0.139 *** $< 2x10^{-16}$	+1.040 *** $1.1x10^{-4}$	-1.392 *** $7.2x10^{-5}$
	Distractor Eccentricity	+0.035 ** $5.5x10^{-3}$	+0.039 n.s. 0.8494	-2.234 *** $< 2x10^{-16}$
	Eccentricity Interaction	+0.005 *** $3.11x10^{-5}$	-0.036 n.s. 0.1282	0.153 *** $5.5x10^{-7}$
	T-D Distance	+0.004 n.s. 0.521	+0.446 *** $1.6x10^{-4}$	-0.915 *** $5.3x10^{-12}$
Long Processing Time	Target Eccentricity	-0.076 *** $4.2x10^{-4}$	+0.168 n.s. 0.4668	-0.316 n.s. 0.1061
	Distractor Eccentricity	-0.015 n.s. 0.4843	+0.261 n.s.ŧ 0.2407	-0.442 * 0.0206
	Eccentricity Interaction	0.004 n.s.ŧ 0.0671	-0.047 *ŧ 0.0313	+0.040 * 0.0338
	T-D Distance	-0.023 * 0.0104	-0.669 *** $2.3x10^{-8}$	+0.074 n.s. 0.511

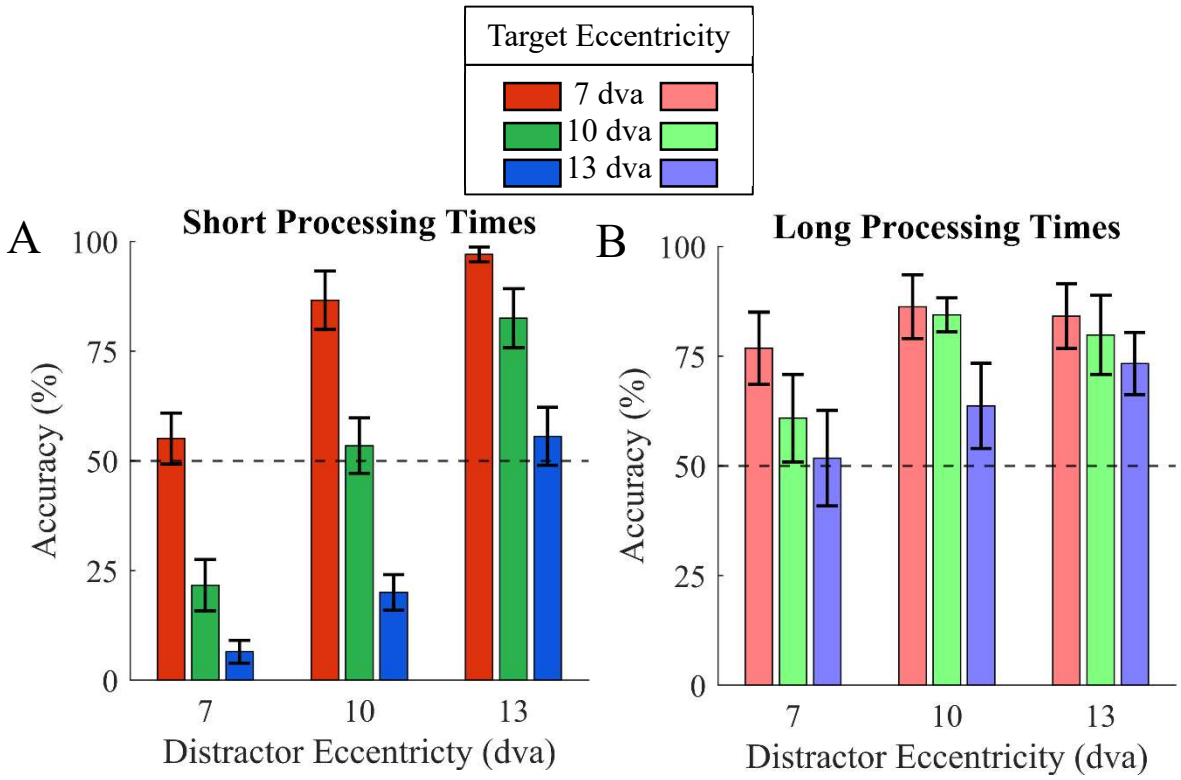


Figure 2: Accuracy by Target and Distractor Eccentricity. The average accuracy plotted over target and distractor eccentricity. A) Accuracy at short processing times while competition between target and distractor is still active. B) Accuracy at long processing times when competition has been resolved. Error bars represent mean ± 95% confidence intervals. The bars and lines are colored according to the target eccentricity of 7 dva (red), 10 dva (green), and 13 dva (blue).

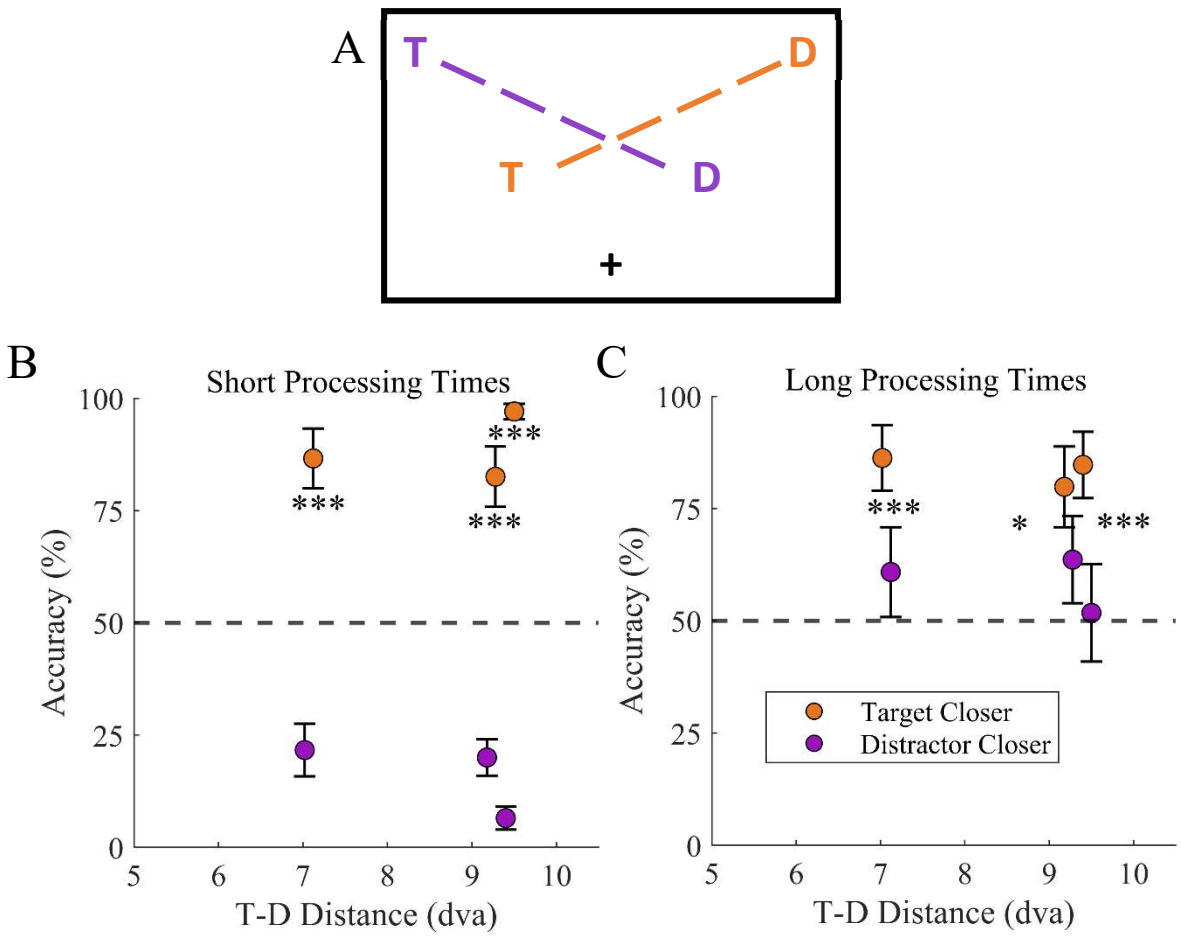


Figure 3: Accuracy by Target-Distractor (T-D) Distance Pairs. A) Example of target and distractor positions that have an equal distance between them (T-D distance) but either the target is closer to fixation (orange), or the distractor is closer to fixation (purple). The average accuracy plotted over T-D distance pairs for B) short processing times, and C) long processing times. Error bars represent mean ± 95% confidence intervals. Note that the pairs are offset slightly for visibility and that the actual T-D distance is between the 2 points. Pairwise comparisons between the allocentric distance pairs are indicated by *: $p < 0.05$ ***: $p < 0.001$.

Saccade Trajectory Deviations

To better understand the reference frames of target and distractor representations, we next investigated their effects on saccade trajectory metrics, which provide a continuous and separable measure of distractor activity and suppression. Separate multiple linear regressions were performed on the saccade curvature and endpoint angle for short and long processing times with target and distractor eccentricity as predictors (see Table 1; Figure 4).

At *short processing* time, both regressions were significant overall (Sum Curvature: $R^2 = 0.0449$, $F(3,3658) = 57.39$, $p < 2.2X10^{-16}$ | Endpoint Angle: $R^2 = 0.0598$, $F(3,3658) = 77.53$, $p < 2.2X10^{-16}$). At short processing time, where saccades deviate towards the distractor, only increasing target eccentricity led to greater saccade curvatures, consistent with an egocentric target representation whose strength diminishes with eccentricity. In contrast, the endpoint angle decreased as the eccentricity of the target and the eccentricity of the distractor increased, again consistent with an egocentric representation. There was also a significant increase in endpoint angle, correlated with the interaction between target and distractor eccentricity, which reflects varying spatial layout of the target and distractor in the display. This would be suggestive of an allocentric effect and will be followed-up on in later analyses.

At *long processing* times, regressions for sum curvature and endpoint angle were both small but significant (Sum Curvature: $R^2 = 0.018$, $F(3,3176) = 19.43$, $p = 1.8X10^{-12}$ | Endpoint Angle: $R^2 = 0.0025$, $F(3,2492) = 3.045$, $p = 0.0037$). Changes to the target eccentricity had no effect on the sum curvature or endpoint angle. The distractor eccentricity was correlated with the endpoint angle, but not the sum curvature. Interestingly, the interaction between target and distractor eccentricity was significantly correlated with both trajectory metrics, again suggesting target-distractor distance effects in an allocentric reference frame. Together, these results show a

decreased strength of egocentric object representations feeding target-distractor competition in saccade planning after the decision-making process has been resolved.

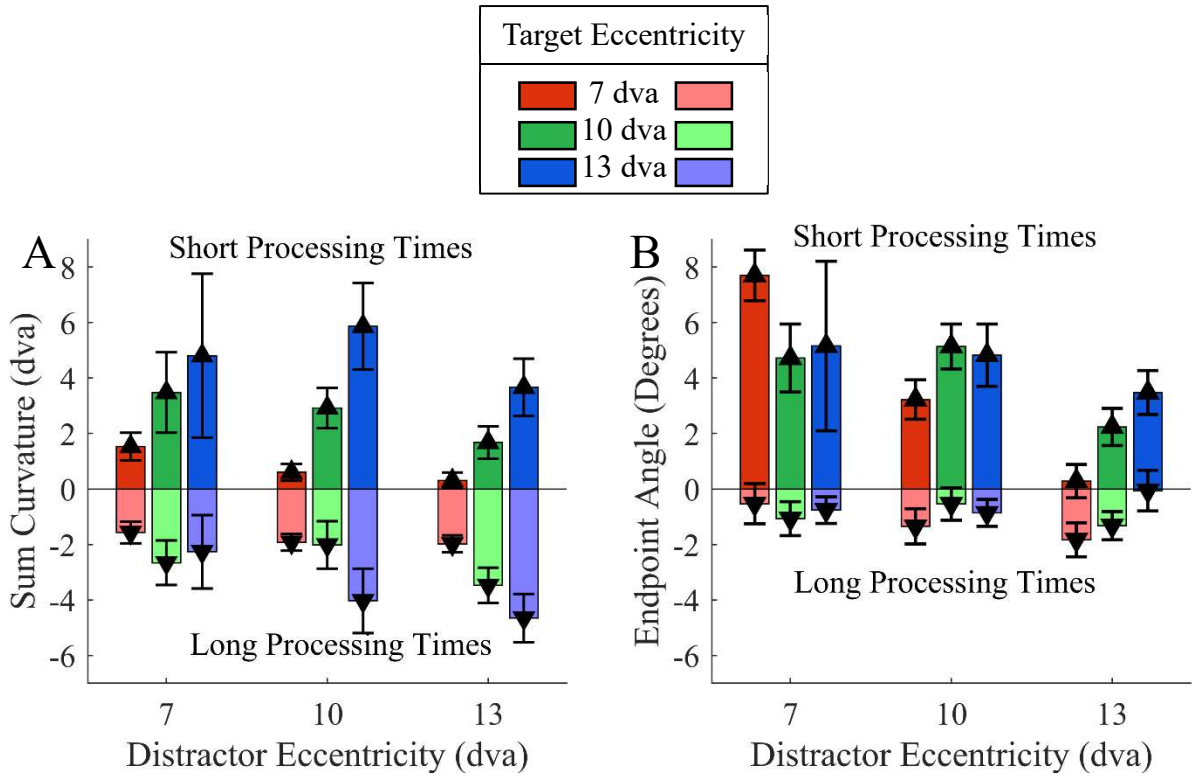
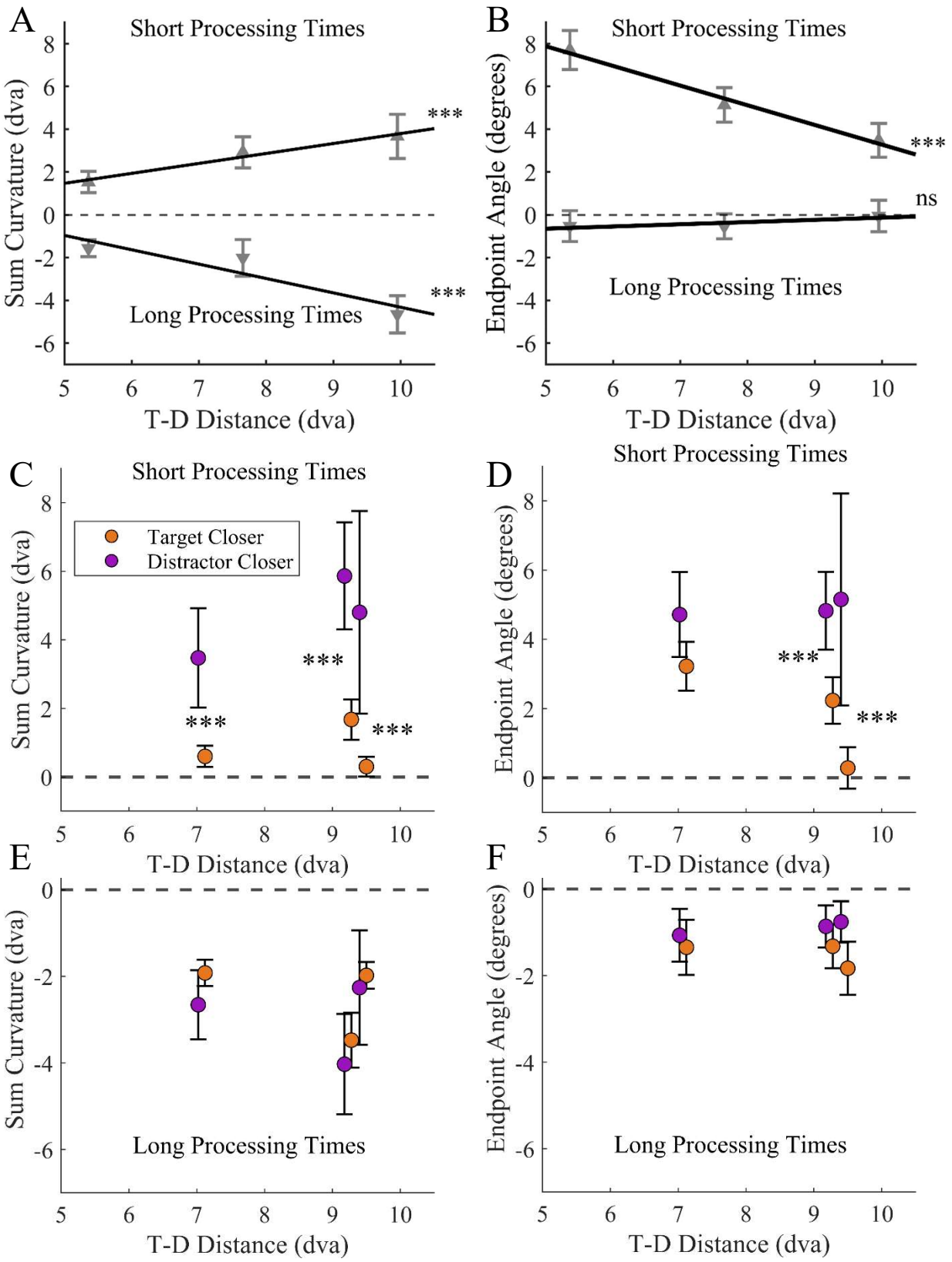


Figure 4: Saccade Trajectory Metrics by Target and Distractor Eccentricity. The average A) sum curvature and B) endpoint angle plotted over target and distractor eccentricity. Error bars represent mean ± 95% confidence intervals. Values above 0 reflect saccade deviations towards a distractor while the decision-making process is active. Values below 0 represent deviations away from the distractor, after object competition has been resolved and the distractor has been suppressed. The bars and lines are colored according to the target eccentricity of 7 dva (red), 10dva (green), and 13 dva (blue).

To investigate the influence of an allocentric reference frame, linear regressions were performed on T-D distance for both saccade metrics when the target and distractor eccentricity were equal (Figure 5 A, B) In addition, pairwise t-tests were used to compare conditions where the T-D distance of the objects was equal, but their eccentricities varied (Figure 5 C-F).

At *short processing* times, T-D distance had a significant effect on both the sum curvature (R^2 = 0.0115, F(1,1231) = 14.37, p = $1.6X10^{-4}$), and endpoint angle (R^2 = 0.0379, F(1,1231) = 48.53, p = $5.3X10^{-12}$). However, pairwise comparisons across equal T-D distances also found significant differences for both metrics (all $p < 0.0032$). Together these findings suggest that at short processing times saccade trajectories are driven by egocentric rather than allocentric representations.

Conversely, at *long processing* times T-D distance was only correlated with the sum curvature (R^2 = 0.0277, F(1,1110) = 31.65, p = $2.3X10^{-8}$), and not endpoint angle (R^2 = 0.0005, F(1,880) = 0.432, p = 0.5112). Pairwise comparisons revealed no differences in sum curvature when target and distractor eccentricities varied while the T-D distance was equal (all $p > 0.2104$), supporting allocentric rather than egocentric effects. There were no effects for saccade endpoint angles when T-D distance was equal across varying target and distractor eccentricities.


A
Short Processing Times
Long Processing Times
Sum Curvature (dva)
T-D Distance (dva)
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B
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Endpoint Angle (degrees)
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C
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Distractor Closer
Sum Curvature (dva)
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Sum Curvature (dva)
Long Processing Times
T-D Distance (dva)
F
Endpoint Angle (degrees)
Long Processing Times
T-D Distance (dva)

Figure 5: Target-Distractor (T-D) Distance. A & B: The average sum curvature and endpoint angle plotted over T-D distance when the target and distractor have equal eccentricity. Values above 0 reflect saccade deviations towards a distractor while the decision-making process is active. Values below 0 represent deviations away from the distractor, after object competition has been resolved and the distractor has been suppressed. C-F: The saccade metrics plotted over T-D distance pairs with the same conventions as in Figure 3, where orange reflects the conditions with the target presented closer to fixation and purple reflects trials with the distractor closer to fixation. Error bars represent mean ± 95% confidence intervals. Note that the pairs are offset slightly for visibility and that the actual T-D distance is between the 2 points. Significant regression effects across T-D distance and comparisons within eccentricity pairs are indicated with ***: $p < 0.001$.

Discussion

In this study, we varied the distance of target and distractor objects relative to a central fixation point, and one another, in a saccadic delayed match to sample task to investigate the reference frame of object-based suppression in the oculomotor system. We found that for short object processing times, while the competition between target and distractor is active[10], both target and distractor are represented in an egocentric reference frame. However, the completion of decision making led to the emergence of distractor suppression, which occurred in an allocentric reference frame.

Saccades executed at short processing times displayed a strong bias for selecting objects closer to fixation (less eccentric). Additionally, the trajectory shifts of these saccades towards the distractor were consistent with weighted vector averaging, as has been previously reported for

saccade deviations towards distracting objects[10][13][29][30][31][32]. Our results for both the saccade trajectories and accuracy suggest that the weight of each object decreases linearly as its eccentricity increases. The strength of this spatial bias alters saccade target selection independent of the identity of the stimuli. Our results lend support to the idea that early saccades are based on bottom-up salience rather than top-down relevance[33] which affects both accuracy and saccade curvature[34]. The eccentricity gradient may result from either an inherent attentional bias[35][36], or reflect a visually-based salience difference (i.e. cortical magnification). Both of these possibilities reflect an egocentric reference frame early in the formation of object representations.

In contrast, long processing times prior to saccade execution resulted in deviations away from the distractor indicating that the distractor had been suppressed[27][29][37][38]. When the stimuli are processed for longer prior to initiating the saccade, the target is identified and we find that the distractor is suppressed in an allocentric reference frame. The magnitude of the curvature is no longer affected by the eccentricity of the distractor. Instead, the magnitude of the curvature increases as the distance between the target and distractor increases, reflecting a shift from an egocentric to allocentric reference frame. However, there continues to be an effect of *target* eccentricity at long processing times, indicating that an egocentric reference frame is still being utilized. This arises from saccades to targets being programmed in egocentric coordinates[14][15]. Object-based suppression in an allocentric reference frame has been found in object-based inhibition of return (IOR)[17][18], and to previous saccade locations[19][20][39][40]. The current work extends these findings, identifying resolution of target/distractor competition as the initiator of distractor suppression that occurs in an allocentric frame of reference.

The stimuli used in our study are similar to alphanumeric characters[27][30], which have previously been suggested to require late-stage ventral stream visual processing in IT cortex where objects are represented allocentrically[24]. The transformation from a gaze-centered reference frame to hand-centered to guide reaching has previously been shown to occur in the PPC[41][42], making it the most probable site for task-relevant reference frame transitions[43]. Therefore, this would suggest that object-based distractor suppression arising in area IT[44] would be carried by projections to posterior parietal cortex (PPC)[45] subsequently feeding into the oculomotor system (i.e. SC, FEF). As PPC is associated with multiple reference frames[46][47][48], it would be able to map allocentric object suppression onto the gaze-centered egocentric reference frame used in saccade planning.

The simultaneous presence of multiple items necessitates discrimination of the target from a distractor. The suppression of the distractor would provide an effective mechanism to improve target selection and motor planning. Our finding that this suppression is allocentric highlights the involvement of object-based distractor inhibition outside of the motor system influencing the saccade planning process. We find that we can measure this allocentric object-based attentional mechanisms in a temporally precise manner manifested through saccade curvatures.

In summary, object-based suppression occurs in an allocentric reference frame affecting target selection and the subsequent motor action. The early representation of potential saccade targets is egocentric and strongly weighted by eccentricity as they compete for selection, with a bias for the object closest to the center of gaze. With longer processing time, the target is identified, and the distractor is suppressed. The target continues to be represented in an egocentric reference frame, while the strength of distractor suppression is dependent on target-distractor distance in an allocentric reference frame. Object-based suppression likely is a general mechanism of visual

processing that affects motor planning, as seen here, as well as perceptual decision making, as seen in prior studies.

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