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Target localization across saccades and at fixation:

Nontargets both facilitate and bias responses

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13   Xiaoli Zhang, and Julie D. Golomb

14   Department of Psychology, The Ohio State University, Columbus, OH 43210, USA

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21   Correspondence should be addressed to:

22   Xiaoli Zhang (zhang.4734@osu.edu) and Julie D. Golomb (golomb.9@osu.edu)

Abstract

The image on our retina changes every time we make an eye movement. To maintain visual stability across saccades, specifically to locate visual targets, we may use nontarget objects as "landmarks". In the current study, we compared how the presence of nontargets affects target localization across saccades and during sustained fixation. Participants fixated a target object, which either maintained its location on the screen (sustained-fixation trials), or displaced to trigger a saccade (saccade trials). After the target disappeared, participants reported the most recent target location with a mouse click. We found that the presence of nontargets decreased response error magnitude and variability. However, this nontarget facilitation effect was not larger for saccade trials than sustained-fixation trials, indicating that nontarget facilitation might be a general effect for target localization, rather than of particular importance to saccadic stability. Additionally, participants' responses were biased towards the nontarget locations, particularly when the nontarget-target relationships were preserved in relative coordinates across the saccade. This nontarget bias interacted with biases from other spatial references, e.g. eye movement paths, possibly in a way that emphasized non-redundant information. In summary, the presence of nontargets is one of several sources of reference that combine to influence (both facilitate and bias) target localization.

Keywords: target localization, landmarks, reference frames, visual stability, spatial perception

Introduction

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43   Starting from the retina, visual information is organized spatially, according to its

44   retinotopic (eye-centered) location. However, this raises a critical problem as we are constantly

45   moving our eyes, and the image received by our retina is changing accordingly, which is not

46   optimal for world-centered (spatiotopic) cognitive tasks. Hence, there is a challenge for our

47   visual system to distinguish real changes in the world from changes on the retina purely caused

48   by eye movements.

49   It has been proposed that we are able to use information from both extra-retinal and

50   retinal sources to achieve visual stability, for example, to localize objects accurately. Extra-

51   retinal sources include corollary discharge or efference copy signals from saccadic eye

52   movements, including the idea that certain visual neurons can use this information to predictively

53   remap their receptive fields, responding to stimuli in their future receptive field locations right

54   before a saccade [1,2]. It has been argued that remapping might be able to compensate for

55   saccade-induced motion, or link the retinal input before and after the saccade to maintain visual

56   stability (reviewed in [3–5]).

57   Another source of stability -- the focus of this project -- is retinal information: i.e., visual

58   information in the scene. One component of retinal information is the saccade target itself; it has

59   been proposed that the saccade target provides critical information for visual stability [6–8].

60   Another retinal component comes from other nontarget objects that appear in the visual field, for

61   example a visual background [6] or frame [9], or other objects that can act as "landmarks" to

62   influence target localization across saccades as well as at fixation [10–13].

63   Here we use the term "nontarget" to refer to visual objects in a display that are presented

64   alongside a "target" object that acts as the fixation or the saccade goal. Researchers often use the

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65 terms "landmarks" or "distractors" to refer to objects presented alongside task targets that

66 influence performance on various tasks. The term "landmark" has been mainly used in fields

67 studying complex real-world tasks such as spatial navigation, and there is a large amount of

68 evidence showing an important role of landmarks in performing navigation tasks (e.g., reviewed

69 in [14]). The word "distractor" is often seen in visual attention studies, for example the influence

70 of different types of distractor items during visual search (e.g., [15,16]). In order to avoid any

71 confusion brought by the existing investigations of these two terms in other fields, here we use

72 the term "nontargets". Hypothetically these nontargets may work as "landmarks" (i.e.,

73 facilitation) or "distractors" (i.e., impairment) in target localization tasks; we use "nontargets" to

74 remain neutral and explore both of these possibilities in our study.

75   Previous studies have investigated the role of nontargets in visuospatial processing in

76 different ways. When participants were asked to saccade to a stimulus flashed during an initial

77 eye movement, their saccade was more accurate when an egocentric cue from a visual nontarget

78 was available [17]. It was also found that the existence of a nontarget as a visual landmark can

79 help guide eye movements to memorized target locations more precisely, showing nontarget

80 facilitation for the memory-based saccade execution [18]. Moreover, the presence of stable

81 nontarget landmarks has been shown to improve detection of target displacement during fixation

82 [19] as well as across saccades ([20] using biological-motion stimuli; [21] using bystander

83 configuration), although nontarget landmarks have failed to facilitate visuospatial tasks in some

84 other domains, such as intrasaccadic perception of relative motion [22].

85   Importantly, nontargets may influence more than just localization accuracy. For example,

86 in target displacement detection tasks, if nontargets displace transsaccadically, it can induce

87 illusory target displacement [10]. In this study, minor displacements of the nontargets

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88   ("landmarks" in the original paper) systematically shifted participants' perception of target

89   displacement, demonstrating that nontargets have an important effect on post-saccadic

90   localization processing, presumably by acting as a stable reference point in trans-saccadic

91   memory; in other words, any change in visual information (specifically, relative position

92   information; also see [23]) compared with pre-saccadic memory was perceived as target

93   displacement, regardless of whether the target actually displaced. This landmark effect may be

94   present both during trans-saccadic tasks and at fixation [12,24].

95   Even when stable, nontargets can also interfere with accurate localization of targets. A

96   phenomenon called compression of space shows that objects tend to be systematically

97   mislocalized around the time of a saccade, such that objects are perceived to be closer to the

98   saccade endpoint than they actually are [25], and likewise the localization of saccade targets can

99   be compressed towards nearby nontarget objects [26]. This mislocalization might result from a

100 "convergent remapping" component of the neuronal remapping process across saccades [27–29],

101 although some other studies suggest that saccade might not be necessary for compression to

102 occur [30]. This bidirectional compression indicates that the location information of nontarget

103 objects may be integrated with target localization, even if nontarget objects only flash briefly.

104 The idea that nontarget location information can interact with or distort target localization has

105 also been found when nontarget objects are continuously presented along with the target. For

106 example, Sheth & Shimojo found that during sustained fixation participants mislocalized a

107 peripheral target as closer to a salient, unfixated bar, which acted as a visual marker [13].

108   In sum, the previous literature has found that the presence of visual landmarks/nontargets

109 may help to localize targets and detect target displacement, as well as potentially bias

110 localization and perceived target displacement. However, most studies have focused on either

111   one effect or the other, or when they have looked at both (e.g. [13]), it has been in the context of

112   peripheral target localization. In the current study, we focus on the localization process of the

113   fixation/saccade target. This is because the saccade target is often critically involved in cognitive

114   processes after saccade execution, such as memory and action [31]; hence, processing location

115   information of the saccade target is an essential cognitive function across saccades. Our first

116   research goal is to ask whether the facilitation and bias effects can be integrated, and how

117   nontarget effects interact with other influences, such as fixation/saccade-related factors. For

118   example, It has been found that localization of a peripheral target can be systematically

119   compressed towards both a nontarget landmark and the current fixation (i.e., "foveal bias") [13].

120   When the fixation point and the visual landmark were on the opposite side of the target, the total

121   response bias was reduced, compared to when they were both on the same side of the target,

122   suggesting that landmarks may facilitate performance by counteracting the foveal bias. Here we

123   systematically investigate how the localization of saccade targets is influenced by nontargets,

124   fixation-related biases, and their interaction (e.g., when they are on the same or opposite side of

125   the target).

126   Second, many patterns of results mentioned above were found regardless of whether a

127   saccade was made or planned. This brings up the question whether nontarget objects influence or

128   facilitate target localization during saccades more than during sustained fixation, given that

129   saccades pose unique challenges for perceptual stability [32]. The answer will tell us more about

130   whether/how nontargets play a particularly important role in visual stability across saccades

131   versus perception more generally. Therefore, we directly compare nontarget effects (facilitation

132   and bias) between saccade and no-saccade trials.

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133   Finally, when nontargets are present during a saccade target localization task, there is

134   also the issue of reference frames: does it matter if nontargets are presented in the same absolute

135   location across the saccade (world-centered reference frame), or should they be manipulated in

136   relative coordinates (eye- or saccade-target-relative reference frame)? Some studies have sought

137   to avoid this issue; for example the nontargets were simply presented on the screen at the same

138   time as the saccade target, but were absent during the initial fixation [10]. This design (which we

139   refer to as the "Baseline" condition in our study) focused on the role of nontargets presented at

140   the time the saccade was triggered. But in real-world processing, nontargets rarely just appear at

141   the time of the saccade. In the current study, we include additional conditions where nontargets

142   are visible from the beginning of the trial (before the saccade cue). Nontargets presented before

143   and after the saccade could remain in the same absolute location on the environment/screen (the

144   "Absolute" condition), or remain in the same location relative to the saccade target (the

145   "Relative" condition). Although the former case is very common and intuitive in daily

146   experiences, many studies have suggested that the latter contains the critical information for

147   nontargets to take effect as landmarks, at least when using displacement judgment tasks ([10];

148   also reviewed in [33]. It has also been found that there might be attention and/or memory

149   benefits for relative spatial location or retinotopic coordinates across saccades, compared to

150   absolute spatial location or spatiotopic coordinates [34–38], although other studies have found

151   evidence for nonretinotopic processing [39–41]. However, it hasn't been directly addressed

152   whether stable nontargets in relative coordinates to the target would provide larger facilitation

153   than in other reference frames.

154   In our project, we employed a modification of target localization tasks used in the

155   literature, where instead of detecting trans-saccadic displacement, we simply had participants

156   perform a target localization task by indicating target location with a mouse click (similar to

157   [13]). Moreover, the more robust free-report task (compared to a two-alternative forced choice)

158   allows us to measure with the response distribution not only whether target localization is

159   facilitated or impaired under different nontarget conditions, but also whether and how much the

160   localization reports are spatially biased by the presence of nontargets (and other factors). We

161   tested target localization under the following conditions: Saccade presence (sustained-fixation vs

162   saccade trials), Nontarget number (0, 1 or 2 nontargets), Congruency of the nontarget location

163   with the initial fixation location (on the same side or opposite sides in relation to the final target)

164   and Reference frame across saccades (Relative: the same location relative to the target; Absolute:

165   the same absolute location on the display screen; and Baseline: not presented before the saccade

166   target). Each reference frame condition was tested in separate experiments; within each

167   experiment all other conditions were intermixed. We hypothesized that the presence of nontarget

168   objects accompanying the target would both facilitate and perhaps bias target localization

169   responses, with our main goal to investigate how this nontarget information interacts with

170   saccade-related information, in different locations and reference frames.

171

Materials and Methods

173   *Participants.* An independent set of sixteen subjects participated in each of the three

174   experiments (E1: 12 females, 4 males, mean age 19.06, range 18-23; E2: 9 females, 7 males,

175   mean age 19.44, range 18-24; E3: 8 females, 8 males, mean age 20, range 18-24). All subjects

176   reported normal or corrected-to-normal vision. They gave informed consent and were

177   compensated with course credit or payment. The study protocols were approved by the Ohio

178   State University Behavioral and Social Sciences Institutional Review Board.

179   Sample size was chosen based on a power analysis of an independent pilot experiment

180   similar to the current study. For the main effect of nontarget (NT) number (0, 1, 2) on response

181   error magnitude, the pilot dataset (N=16) had an effect size of η_p^2=0.493, and the power to detect

182   such an effect was estimated as .999. We thus set N=16 as the sample size for all experiments.

183

184   *Apparatus.* The experiment was run using Psychtoolbox [42] in Matlab (MathWorks).

185   Stimuli were presented on a 21-in. CRT monitor with a refresh rate of 85 Hz. Participants were

186   seated 61 cm in front of the monitor in a dark testing room, with a chinrest for eye-tracking

187   purposes.

188

189   *Eye-tracking.* Eye positions were recorded throughout the experiment using an Eyelink

190   1000 Eye Tracker at 500 Hz. Eye position data were used to ensure the participants kept their

191   eyes on the target, and to measure saccade trajectories and latencies. If they were not fixating at

192   the correct location, a "Fixation Error!" message was shown on the screen, the current trial failed

193   immediately, and the next trial started. The failed trials were re-run in a random order later in the

194   block. Saccades were identified and analyzed using custom Matlab code as described below.

195

196   *Task procedure.* Three experiments were run to look at the effect of nontargets on target

197   localization across saccades and at fixation. The paradigm is shown in Fig 1.

198

199   ***Fig 1 Experiment Paradigm.*** *A) Sample trial sequence for each of the three experiments. Each example*

200   *shows a rightward saccade trial with 2 nontargets (white circles) on the right side. In E1 the nontargets*

201   *appear at the same time as the saccade cue. In E2 and E3 the nontargets are present from the beginning*

202   *of the trial and maintain the same locations relative to the saccade target (E2) or absolute screen*

203   *location (E3). After subjects successfully complete the saccade, the target is removed for a 200ms delay,*

204   *and then participants make a response by moving the cursor and clicking at the remembered final target*

205   *location. Feedback (a red cross at the reported location and a white cross at the correct location) was*

206   *presented after response. B) Schematic indicating the different possible saccade patterns. Crosses*

207   *indicate the three possible target locations, and arrows show saccade patterns; note that the actual target*

208   *locations were jittered on each trial. C) Schematic showing different conditions of congruency on a*

209   *sample saccade trial. Black crosses indicate the initial fixation and white crosses indicate the saccade*

210   *target location. For a rightward saccade, NTs could appear either to the left or right of the final target.*

211   *Left panel: when NTs and the initial fixation location were to the left of the final target location, this*

212   *would be a same-side condition. Right panel: when NTs were to the right and the initial fixation location*

213   *was to the left of the final target location, this would be an opposite-side condition. Dashed rectangle*

214   *indicates the possible extent of the NT region; the actual nontargets (circles) were randomly presented in*

215   *that rectangle region in each trial.*

216

217   For all experiments, participants began each trial by fixating a white cross sized

218    $0.2° \times 0.2°$ (the target) on a constant gray background, RGB (127, 127, 127). The horizontal

219   location of the target was randomized among three possible locations – 4° left of, 4° right of, and

220   on the vertical midline, with 0° - 0.25° additional random jitter. The vertical location was also

221   jittered within 0.25° above or below the horizontal midline of the screen. Once participants were

222   fixating (i.e., the eye location stayed within 1.5° range of the target), the target stayed visible for

223   a variable period of 500 to 1000 ms. On saccade trials (50% of all trials), the target then jumped

224   to an adjacent location to trigger a horizontal saccade of 4° (Fig 1B). The saccade end time was

225   determined when the participants' eye position was within 1.5° range from the saccade target and

226   the velocity of the eye movement was below 30°/s [43]. Trials failed immediately if the saccade

227   was not completed within 3 s after the target jump.

228   After the saccade was detected as completed, the target was removed for 200 ms. This

229   means that the target was removed post-saccadically, but not midflight. Note that the goal of this

230   design is to not to investigate trans-saccadic perception per se, but how target localization before

231   and after saccades is affected by the presence of nontargets. On no-saccade trials, the target was

232   removed from its initial location after a delay analogous to saccade latency (250 – 300 ms).

233   Following this 200ms blank interval, a beep sound occurred to instruct participants to respond by

234   moving the cursor to the remembered target location – the center of the cross. The cursor was

235   presented on the screen at a random starting point 0.5° to 1° away from the target, to eliminate

236   the effect of cursor location across trials. Participants clicked the left button to register their

237   response. Feedback with the correct and reported location was shown for 1000 ms.

238   On some trials, nontarget objects (white empty circles of 0.2° radius) were also presented

239   during the trial: trials were equally distributed among 0, 1, or 2 NTs. Participants were told that

240   they should complete the task on the target cross, and that the circles were irrelevant to their task.

241   In Experiment 1 (Baseline), nontargets appeared on the screen simultaneously with the saccade

242   target (second fixation cue), or after an analogous delay on no-saccade trials. In Experiments 2 &

243   3, nontargets appeared at the beginning of the trial, and remained on the screen throughout the

244   trial in either "Relative" (Experiment 2) or "Absolute" (Experiment 3) reference frames. In

245   Experiment 2, nontargets remained in the same location relative to the fixation cross (i.e., they

246   moved with the saccade target; see Fig 1). In Experiment 3, nontargets remained in the same

247   absolute location on the screen across the saccade.

248   In all three experiments, we designed the *NT location* conditions to be either to the left or

249   right of the target's final position, and thus either on the same side or opposite side as the initial

250   fixation on saccade trials (Fig 1C). The actual NT locations were randomized for each trial

251   within an imaginary vertical rectangle zone of $1° \times 2°$, centered $2°$ to the left or right of the target.

252   This means that on trials with 2 NTs, these two NTs were both presented on the same side of the

253   target. In the Baseline experiment, NTs were presented when the target appeared in its final

254   position, centered $2°$ to the left or right of that final target location. In the Relative experiment,

255   the NTs first appeared centered $2°$ to the left or right of the initial target location, and moved

256   with the target to remain in the same relative location. Note that because the NTs moved with the

257   target instead of the eyes, we call this condition "relative" instead of "retinotopic". In the

258   Absolute experiment, we included three different scenarios (S3A Fig). For rightward saccades,

259   these scenarios were as follows: (a) the NTs appeared centered $2°$ to the right of the initial target

260   position, which made them $2°$ to the left of the final target position ("near-near"); (b) the NTs

261   appeared $2°$ to the left of the initial target position, meaning $6°$ to the left of the final target

262   position ("near-far"); (c) the NTs appeared $6°$ to the right of the initial target position, meaning

263    $2°$ to the right of the final target position ("far-near"). It is an intrinsic confound in the Absolute

264   experiment that the distance between NTs and the target could not be kept at $2°$ before and after

265   a saccade and still include a mix of same-side and opposite-side conditions. Therefore, we

266   included all three distance conditions described above to cover both same-side and opposite-side

267   conditions in the Absolute experiment. For the main analyses, we collapsed across these three

268   distance conditions. Separate results for the three distance conditions are shown in the

269   supplementary materials.

270   For all experiments, participants completed a practice block, and then there were 12 main

271   task blocks, 48 trials each. These 48 trials were equally distributed among the 2 saccade presence

272   (no-saccade and saccade) $\times$ 3 NT number (0, 1 and 2 NTs) $\times$ 2 NT location (same and opposite

273   side relative to initial fixation). A minimum of 8 blocks was set as a threshold for the data to be

274   included in analyses (some participants could not complete the full 12 blocks in the allotted 1.5-

275   hour session due to eye tracking difficulty). Each subject thus completed 32-48 trials per critical

276   condition described above.

277

278   *Data processing and analyses*. Data were processed with custom Matlab (version 2015b)

279   code and analyzed in JASP [44]. Trials with unreasonably long reaction time (>7s) or

280   unreasonably large localization error (>1.5°) were discarded. The latter means that the situation

281   where participants mistook the NT location as the target location was excluded. The discarded

282   trials took up less than 0.2% of all trials in each experiment.

283   The conditions we analyzed included saccade presence (no-saccade and saccade), NT

284   number (0, 1 and 2 NTs), and NT location (same and opposite side relative to initial fixation

285   location). Each of these conditions was tested within each experiment (within-subjects), and

286   compared across experiments (between-subjects), which varied reference frame.

287   Our primary goal was to assess how the above factors influence target localization

288   performance; thus, the analyses primarily focus on the participants' mouse responses (though we

289   include some additional analyses of eye-tracking data in the supplementary materials). We first

290   investigated how making saccades influences target localization by comparing saccade versus

291   no-saccade trials; then how NTs influence target localization by comparing trials with zero, one

292   and two NTs; and finally, if/how these saccade and NT influences interact by analyzing saccade

293   trials with NTs. We used three measurements to quantify target localization outcomes: 1) how

294   accurate participants' responses were, by calculating the mean error magnitude as the distance

295   (i.e., absolute value) between the reported and correct target location; 2) how variable

296   participants' responses were, by calculating the root mean squared distance (RMSD) for each

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297   condition of interest for each subject; 3) how biased participants' responses were, by calculating

298   the mean directional error vector along the horizontal axis along which saccades and NT

299   locations were manipulated.

300   Specifically, RMSD was calculated using the formula:

301
$$\text{Variability} = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}((x_i - \bar{x})^2 + (y_i - \bar{y})^2)}$$

302   where for each subject each condition, (x_i, y_i) is the response coordinates for trial i,

303   centered around the actual target location; $(\bar{x}, \bar{y})$ is the average coordinates of all responses in

304   that condition; n is the number of trials, and the denominator (n-1) is the degree of freedom to

305   get an unbiased estimate.

306   All of the above three measurements were calculated in units of visual angle. We used

307   ANOVAs and t-tests for statistical analyses; effect sizes were calculated using η_p^2 and Cohen's

308   d. Greenhouse-Geisser correction for violations of sphericity and Holm–Bonferroni correction

309   for multiple comparisons were used when necessary.

310

Results

312   Our research question focused on how saccades and nontargets influence target

313   localization independently and interactively.

314   A descriptive plot of participants' responses is depicted in Fig 2, where a scatter plot of

315   participants' responses in each trial is plotted relative to the correct target location and saccade /

316   NT directions, and 95% confidence ellipses of response error summarize the accuracy, precision,

317   and bias of these responses (error ellipses calculated according to [45]). Statistical comparisons

318   for each question of interest follow in the sections below.

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319

320   *Fig 2 Scatter plots of participants' localization errors across conditions in each experiment. X and y*

321   *axes represent response error (in degree visual angle, dva) on horizontal and vertical axes respectively.*

322   *(0,0) is the correct target location. Error ellipses show the 95% confidence interval of covariance*

323   *between response errors on x and y axes. All trials were aligned according to the schematics above each*

324   *column. The cross indicates the final target; the dashed rectangle indicates the range of nontarget (NT)*

325   *location; the arrow indicates saccade direction. Note that the schematics are not drawn to scale or in the*

326   *same scale as the scatter plots; for reference, the majority of responses were made within 0.5deg of the*

327   *target, the closest NTs were 1.5deg from the target, and the initial fixation was 4deg from the target. The*

328   *first column shows no-saccade trials. The second and third columns show saccade trials when NTs and*

329   *the initial fixation location were on opposite sides of the target and when they were on the same side of*

330   *the target, respectively. Rows correspond to the 3 experiments. Within each plot, data are shown for 0, 1,*

331   *and 2 NTs, including all participants for visualization. N=16 for each experiment.*

332

Accuracy of target localization

334   We first looked at the effects of saccades and NTs on overall target localization accuracy,

335   measured by the mean magnitude of error (distance) between the correct and reported locations.

336   Note that this initial measure doesn't include information on which direction the participants

337   made the error. Data were submitted to a 2 (saccade presence: 0, 1) × 3 (NT number: 0, 1, 2) × 3

338   (experiment: 1, 2, 3) mixed-design ANOVA.

339   The results showed a significant main effect of saccade presence, $F(1,45)=15.351$,

340   $p<.001$, $\eta_p^2=.254$, indicating that the error magnitude was larger in saccade trials than no-saccade

341   trials. There was also a main effect of NT number, $F(1.503,67.662)=46.809$, $p<.001$, $\eta_p^2=.510$,

342   that increasing the number of NTs decreased the error magnitude. There was no significant

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343   interaction between saccade presence and NT number, $F(1.647,74.111)=0.059$, $p=.913$, $\eta_p^2=.001$,

344   indicating that the influence of NTs on target localization accuracy was similar for both saccade

345   and no-saccade trials.

346   Do these influences of NTs and saccades vary across our different experiments? In

347   Experiment 1 (baseline), NTs were presented at the same time as the saccade target, whereas in

348   Experiments 2 and 3 NTs were presented before the saccade target, in relative (same location

349   relative to target) and absolute (same absolute location on screen) coordinates, respectively. We

350   found a significant interaction between experiment and NT number, $F(3.005,67.622)=4.201$,

351   $p=.009$, $\eta_p^2=.157$, but no significant main effect of experiment nor interaction between saccade

352   presence and experiment, $F(2,45)=1.338$, $p=.273$, $\eta_p^2=.056$, $F(2,45)=1.211$, $p=.307$, $\eta_p^2=.051$.

353   There was no significant three-way interaction between saccade presence, NT number and

354   experiment, $F(3.294,74.111)=1.833$, $p=.143$, $\eta_p^2=.075$. Fig 3A illustrates the NT number $\times$

355   experiment interaction. The presence of NTs decreased error in all experiments, but this NT

356   facilitation effect was greater for the baseline and relative conditions (E1 and E2) compared to

357   the absolute condition (E3). Using the zero NT trials as a baseline for each experiment, we

358   calculated the "NT facilitation" effect for NT1 and NT2 trials for each of the 3 experiments. A 2

359   (NT number: 1, 2) $\times$ 2 (saccade presence: 0, 1) $\times$ 3 (experiment: 1, 2, 3) mixed-design ANOVA

360   found a significant main effect of NT number, $F(1,45)=6.914$, $p=.012$, $\eta_p^2=.133$, showing greater

361   facilitation with two nontargets than one nontarget, along with a main effect of experiment,

362   $F(2,45)=5.206$, $p=.009$, $\eta_p^2=.188$. Post hoc t-tests between experiments showed that NT

363   facilitation was not significantly different between baseline and relative conditions, $t(30)=-0.447$,

364   $p=.658$, Cohen's $d=-0.158$, but that in both baseline and relative conditions facilitation effects

365   were significantly larger than in the absolute condition ($t(30)=-3.920$, $p<.001$, Cohen's $d=-1.386$

366   and $t(30)$=-2.477, p=0.019, Cohen's d=-0.876, respectively). It is possible that some of these

367   experiment effects could be driven by distance effects – i.e. in the absolute condition some

368   nontargets were located further from the target (see methods). We then restricted Absolute trials

369   to the subset that matched the distance of relative NTs (i.e., "near-near" condition), and we still

370   found a significant difference between Absolute and Relative facilitation, $F(1,15)$=6.712,

371   p=.020, η_p^2=.309 (additional results in the supplementary materials).

372

373   ***Fig 3 Target localization performance.*** *Target localization error magnitude (A) and response variability*

374   *(B) as a function of NT number, in each of the three experiments. Data are collapsed across saccade and*

375   *no-saccade trials. N=16 for each experiment. Error bars are SEM.*

376

Variability of responses

378   We next examined another important measurement of target localization performance,

379   the variability of the responses, quantified using RMSD.

380   We did similar analyses as above, using a 2 (saccade presence: 0, 1) × 3 (NT number: 0,

381   1, 2) × 3 (experiment: 1, 2, 3) mixed-design ANOVA, and found similar patterns. There was a

382   significant main effect of NT number, $F(1.625,73.108)$=52.783, p<.001, η_p^2=.540, where NTs

383   reduced response variability. Making a saccade significantly increased response variability,

384    $F(1,45)$=13.133, p<.001, η_p^2=.226. There was no significant interaction between saccade

385   presence and NT number, $F(1.670,75.132)$=2.059, p=.142, η_p^2=.044.

386   There was no significant interaction between saccade presence and experiment,

387    $F(2,45)$=0.955, p=.392, η_p^2=.041. The NT number × experiment interaction was significant,

388    $F(3.249,73.108)$=3.984, p=.009, η_p^2=.150. As shown in Fig 3B, NT facilitation affected

17

389   variability in a similar way as overall accuracy. NT facilitation was present in all three

390   experiments, but was greater for the baseline and relative conditions (E1 and E2) compared to

391   the absolute condition (E3), $F(2,45)=5.503$, $p=.007$, $\eta_p^2=.197$, and was greater for 2NT than

392   1NT, $F(1,45)=7.300$, $p=.010$, $\eta_p^2=.140$. Similar to accuracy analyses above, when restricting to

393   trials in which NT distance was comparable across experiments, Relative facilitation was still

394   greater than Absolute facilitation, $F(1,15)=7.405$, $p=.016$, $\eta_p^2=.331$.

395

Spatial response biases

397   So far, we assessed the performance of target localization in terms of error magnitude and

398   response variability, and found that the presence of nontargets decreased both measurements; i.e.

399   nontargets improved target localization performance on both saccade and no-saccade trials.

400   However, it should be noted that these two measurements ignored the directional information of

401   participants' responses. That is, were errors randomly distributed around the correct location, or

402   was there systematic variability? There could be two ways in which directional error might be

403   informative here: First, there might be a difference in horizontal versus vertical error magnitudes

404   (particularly because in our paradigm, saccade direction was only manipulated along the

405   horizontal axis). Second, we can ask whether the saccade direction and/or location of the NTs on

406   a given trial might systematically *bias* the reported target location, e.g. toward or away from the

407   NTs or initial fixation.

408   To address the first question, we performed the same analysis as above for mean error

409   magnitude, but now separately for horizontal and vertical error magnitude. The increase in error

410   on saccade versus no-saccade trials happened only along the horizontal axis; interestingly,

411   making a saccade actually decreased the error along vertical axis (horizontal: $F(1,45)=28.288$,

18

412    $p<.001$, $\eta_p^2=.386$; vertical: $F(1,45)=10.791$, $p=.002$, $\eta_p^2=.193$). NT facilitation happened along

413   both horizontal and vertical axes. However, the experiment × NT interaction was only found

414   along the horizontal axis (horizontal: $F(3.017,67.893)=5.009$, $p=.003$, $\eta_p^2=.182$; vertical:

415    $F(3.592,80.825)=0.909$, $p=.454$, $\eta_p^2=.039$). Similar patterns were found for response variability:

416   making a saccade increased response variability only along the horizontal axis (horizontal:

417    $F(1,45)=18.362$, $p<.001$, $\eta_p^2=.290$; vertical: $F(1,45)=0.740$, $p=.394$, $\eta_p^2=.016$); and NT

418   facilitation existed along both horizontal and vertical axes, but interacted with experiment only

419   along the horizontal axis (horizontal: $F(3.279,73.781)=5.065$, $p=.002$, $\eta_p^2=.184$; vertical:

420    $F(3.782,85.098)=0.542$, $p=.695$, $\eta_p^2=.024$).

421   Because saccades were only executed along the horizontal axis, and the NT x experiment

422   interaction was also specific to the horizontal axis, for our second question (i.e., spatial bias), we

423   focused primarily on horizontal directional error. To enable us to look at the joint influence of

424   saccade and NT biases, we simplified the location of NTs into whether they were presented in

425   the same horizontal direction as the initial fixation (Same) or opposite horizontal direction

426   (Opposite).

427   *Does saccade direction bias target localization?* To isolate a potential saccade-related

428   bias, we first restricted our analyses to trials with zero NTs (Fig 4B and 4C, when NT number is

429   zero in saccade trials; also S1B Fig). We aligned each trial's data so that a positive error vector

430   would mean bias towards the initial fixation location on saccade trials (and towards right on no-

431   saccade trials). A 2 (saccade presence: 0, 1) × 3 (experiment: 1, 2, 3) mixed-design ANOVA

432   found a significant main effect of making a saccade, $F(1,45)=54.863$, $p<.001$, $\eta_p^2=.549$, with

433   participants' responses more biased on saccade than no-saccade trials. Post-hoc tests revealed

434   that on saccade trials, target localization (mouse) responses were significantly biased towards the

19

435   initial fixation location (compared to zero bias: $t(47)$=-7.482, p<.001, Cohen's d=-1.080), while

436   the bias on no-saccade trials was not significantly different from zero $t(47)$=0.879, p=.384,

437   Cohen's d=0.127. There was no significant main effect of or interaction with experiment,

438    $F(2,45)$=0.311, p=.734, η_p^2=.014, $F(2,45)$=0.351, p=.706, η_p^2=.015, respectively. A

439   supplementary analysis (S1 Fig) revealed that there was also a similar bias in saccade landing

440   point, with the majority of saccade trials undershooting the target. However – critically – target

441   localization (mouse response) was biased towards the initial fixation location regardless of actual

442   saccade endpoint. We compared saccade undershoot and overshoot trials separately and found

443   that for both saccade undershoot and overshoot trials, there was a significant localization bias in

444   the direction of initial fixation in all experiments, t's≥2.802, p's≤.013, Cohen's d's≥0.700; i.e.,

445   saccade endpoint (undershoot or overshoot) impacted the magnitude of this bias, $F(1,45)$=9.102,

446   p=.004, η_p^2=.168, but did not drive the effect.

447

448   ***Fig 4 Spatial response biases.** A) Response biases on no-saccade trials (NT-related bias). Positive values*

449   *mean biasing towards NT location (and towards right when NT number is zero). Bias increases with NT*

450   *number. B) Response biases on saccade trials when NT location and initial fixation are on the opposite*

451   *sides of the target. Positive values mean biasing towards the initial fixation location. When the NT*

452   *number is zero, the positive values in three experiments indicate a saccade-related response bias towards*

453   *the initial fixation. NTs on the opposite side counteract this bias. C) Response biases on saccade trials*

454   *when NT location and initial fixation are on the same side of the target. As in B, when the NT number is*

455   *zero, the positive values in three experiments indicate a saccade-related response bias towards the initial*

456   *fixation. However, NTs on the same side add little to this bias. N=16 for each experiment. Error bars are*

457   *SEM.*

458

459   *Do nontargets bias target localization?* Next, to explore the potential bias from

460   nontargets alone, we looked at no-saccade trials, comparing zero, one or two NTs (Fig 4A). We

461   aligned the data so that a positive error vector would mean bias towards the NTs (along

462   horizontal axis). A 3 (NT number: 0, 1, 2) × 3 (experiment: 1, 2, 3) mixed-design ANOVA found

463   a significant main effect of NT number, $F(1.425,64.144)=13.062$, $p<.001$, $\eta_p^2=.225$. On trials

464   where NTs were present, participants' responses were biased towards the NT location; the bias

465   was significant for both 1NT and 2NT, $t(47)=5.879$, $p<.001$, Cohen's $d=0.849$, $t(47)=9.242$,

466     $p<.001$, Cohen's $d=1.334$, respectively, and two NTs yielded a significantly larger bias than one,

467     $t(47)=2.645$, $p=.011$, Cohen's $d=0.382$. There was no significant main effect of or interaction

468   with experiment, $F(2,45)=1.791$, $p=.179$, $\eta_p^2=.074$, $F(2.851,64.144)=0.541$, $p=.647$, $\eta_p^2=.023$,

469   respectively.

470   *Joint influence of saccade and NTs.* Now the key question is: how do these two sources

471   of bias *interact* when both are present? E.g., if the biases induced by the saccade and the NTs are

472   in the same direction, do they add together to result in a larger bias? If the sources of bias are in

473   opposite directions, do they counteract each other? In other words, can the presence of non-

474   targets compensate for the bias induced by the saccade? For this analysis, we separated saccade

475   trials into cases where the initial fixation and the NTs were on opposite sides of the target

476   (*Opposite side* condition, Fig 4B), or on the same side of the target (*Same side* condition, Fig

477   4C). We conducted a 3 (NT number: 0, 1, 2) × 2 (Congruency: same side, opposite side) × 3

478   (experiment: 1, 2, 3) mixed-design ANOVA on the saccade trials; in order to make the ANOVA

479   feasible, we dummy-coded saccade trials with zero nontargets to be randomly assigned to the

480   same or opposite side.

481   We found a significant main effect of NT number, $F(1.375,61.869)=24.911$, $p<.001$,

482    $\eta_p^2=.356$, showing that overall the presence of nontargets biased responses towards the NT

483   location, as before for the no-saccade trials. There was a significant main effect of congruency,

484    $F(1,45)=49.892$, $p<.001$, $\eta_p^2=.526$, and a congruency × NT number interaction,

485    $F(1.593,71.665)=39.222$, $p<.001$, $\eta_p^2=.466$. There were also significant Experiment × NT

486   number and Experiment × Congruency interactions, $F(2.750,61.869)=5.740$, $p=.002$, $\eta_p^2=.203$

487   and $F(2,45)=7.774$, $p=.001$, $\eta_p^2=.257$, respectively. The 3-way interaction between NT number,

488   experiment and congruency was not significant, $F(3.185,71.665)=1.970$, $p=.123$, $\eta_p^2=.080$.

489   To better explore these interactions, we separated the same side and opposite side trials

490   and did a 3 (NT number: 0, 1, 2) × 3 (experiment: 1, 2, 3) mixed-design ANOVA on each. When

491   NTs were on the same side as the initial fixation (Fig 4C), there was a relatively stable positive

492   response bias (i.e., toward the initial fixation); there was no significant main effect of NT number

493   or experiment, nor NT number × experiment interaction, all F's≤1.905, p's≥.167, η_p^2's≤.061.

494   This implies that when NTs were presented on the same side of the target as the initial fixation,

495   there was no additivity of the biases; the magnitude of the bias on these trials was the same as the

496   saccade-related bias alone on 0-NT trials.

497   However, when NTs were on the opposite side of the target as the initial fixation (Fig

498   4B), we found a significant main effect of NT number, $F(1.498,67.408)=53.383$, $p<.001$,

499    $\eta_p^2=.543$, a significant main effect of experiment, $F(2,45)=6.180$, $p=.004$, $\eta_p^2=.215$, and a

500   significant interaction, $F(2.996,67.408)=5.495$, $p=.002$, $\eta_p^2=.196$. The addition of the NTs here

501   seemed to counteract the saccade-related bias coming from the opposite direction, with the

502   influence of 2 NTs significantly greater than 1 NT, $t(47)=3.027$, $p=.004$, Cohen's $d=0.437$.

503   Interestingly, the degree to which the NTs counteracted the saccade-related bias varied by

504   experiment. In the Baseline experiment (E1), the saccade-related bias appeared to be completely

505   counteracted by the opposite-side NTs; the response bias when NTs were present was not

506   significantly different from zero, $t(15)$=-0.713, p=.487, Cohen's d=0.178 (post-hoc t-test

507   collapsing across 1 and 2 NTs), suggesting equal and opposite contributions from the NT-related

508   and saccade-related biases. In the Relative experiment (E2), the NT influence seemed to exceed

509   the saccade-related bias; here the response bias was significantly negative (towards NTs, away

510   from initial fixation), $t(15)$=-4.312, p=.002, Cohen's d=1.078, in such a way that the NT-related

511   bias overcompensated saccade-related bias. In contrast, in the Absolute experiment (E3), the NT-

512   related bias did not fully counteract the saccade-related bias; here the response bias was still

513   significantly positive (towards initial fixation), $t(15)$=2.809, p=.026, Cohen's d=-0.702. For these

514   three t-tests, P values were corrected for multiple comparisons using Holm–Bonferroni

515   correction. This pattern of results implies that the bias induced by the presence of NTs was more

516   influential when NTs were presented in the relative reference frame than absolute reference

517   frame across saccades.

518

Discussion

520   In the current study, we tested how the presence of nontargets influences target

521   localization across saccades and during sustained fixation. Unsurprisingly, we found that target

522   localization performance was generally worse on saccade than no-saccade trials (in terms of

523   mean error magnitude and response variability), and the presence of nontargets improved target

524   localization performance. The presence of nontargets exerted comparable facilitation effects on

525   saccade trials and no-saccade trials, suggesting that the facilitation effect is a more general visual

526   effect rather than of particular importance to saccadic stability. We also measured response bias

527   (directional error), finding that participants' responses were biased towards both the initial

528   fixation location (saccade-related bias) and the NT locations. These two sources of bias

529   interacted in an interesting way: When both sources fell on the same side of the target they were

530   not additive, but when they fell on opposite sides of the target, the NT bias counteracted the

531   saccade-related bias. For both facilitation and bias effects, the influence of nontargets was

532   stronger when there were 2 NTs than 1 NT, and was weaker in the absolute than relative and

533   baseline experiments. Below we discuss the implications of each of these findings.

534

Saccade influence on target localization

536   A large literature has focused on the challenge of maintaining visual stability while

537   moving the eyes around, particularly in terms of target localization abilities. In all three

538   experiments, we found that saccades impaired performance by increasing error magnitude as

539   well as response variability, even though the target was fixated within the fovea, where visual

540   acuity and overt attention is the highest. The saccade-related increase in error magnitude and

541   response variability happened only along the horizontal axis, such that the location errors

542   become elongated along the saccade axis. This basic finding is intuitive, and is consistent with

543   previous findings [10,13,24].

544   In addition to a generic saccade-related decrease in performance, we also found a

545   systematic saccade-related bias: participants' responses were on average biased in the opposite

546   direction of the saccade. There are three possible sources of this saccade-related bias: bias

547   towards the screen center, bias towards the actual saccade landing position, and/or bias towards

548   the initial fixation location. In our design, the potential effect of screen center location was

24

549   controlled – a left/right saccade could be from center to periphery on the screen or vice versa

550   (Fig 1) – so the screen center is not likely to be the source of this saccade-related bias. The

551   second and third possibilities, however, could both have predicted a systematic response bias in

552   the same direction as we found: as reported above, both the eye landing position and the mouse

553   responses were biased towards initial fixation on average. However, the analysis differentiating

554   the influence of saccade landing position and initial fixation location revealed that while saccade

555   landing position did modulate the magnitude of response bias, there was still a significant bias

556   towards the initial fixation location even on overshoot trials when the actual eye position was in

557   the opposite direction of the target. Thus, while actual current eye position may induce some bias

558   (similar to the influence of saccade landing site on perception of the target displacement, shown

559   in [46]), the primary source of the saccade-related response bias here seems to be the initial

560   fixation location. Participants may have been using the pre-saccadic fixation location as a visual

561   or oculomotor reference, and target localization responses were biased towards this reference;

562   however, participants were not simply clicking on the location that they looked at.

563   Our result is consistent with a number of previous studies demonstrating a response bias

564   towards the current and/or initial fixation locations [13,36,47]. Sheth and Shimojo found that

565   visual memory of peripheral spatial locations can be biased towards the current fixation (i.e.,

566   "foveal bias") over time, independent of saccade preparation or saccade execution. They

567   proposed that this bias likely happens during encoding period when the eccentricity of the target

568   might be underestimated [13]. A response bias towards the initial fixation location has also been

569   found across saccades, when participants retained spatial memory of a peripheral target [36]. It

570   should be noted that our design differed from these previous studies in that instead of a

571   peripheral target, our target was the saccade target to be fixated on. However, we propose that

25

572   the saccade-related bias in our result likely happened in a similar way as the studies mentioned

573   above. When the saccade target location was presented on the screen while participants were still

574   fixating on the initial fixation, the saccade target was indeed in the periphery at that time point.

575   Due to the underestimated eccentricity during the encoding process, a biased representation of

576   space was likely created and maintained across the saccade. Therefore, we still found "foveal

577   bias" – bias towards the initial fixation, after the saccade was completed. Indeed, the magnitude

578   of saccade-related bias we found (0.05°) is much smaller than the foveal bias in [13] (about 1°),

579   and this is likely due to the acuity difference between processing foveal and peripheral targets.

580

Nontarget facilitation on both error magnitude and response variability

583   The influence of nontargets on target localization has been investigated in many studies,

584   including the presence of nontargets on saccade execution accuracy [18] and the effect of NT

585   displacement on target displacement perception [10,19–21,24]. In our study, we focused on the

586   influence of nontargets on target localization in a more systematic manner: investigating the

587   number, location and reference frame of nontargets. We found that the presence of stable

588   nontargets in general facilitated performance, by decreasing the mean error magnitude as well as

589   response variability. The magnitude of NT facilitation was small in absolute terms (about 0.025°

590   or 1 pixel), but reflected an improvement of approximately 14% of the baseline for absolute error

591   measurement, and 12% for response variability measurement. The correct target location landed

592   in the fovea, and there were other potential references such as the display boundaries; therefore,

593   even an improvement of 1 pixel is a meaningful benefit provided by the presence of nontargets.

594   Did the NT facilitation stem from a direct effect – i.e. a more precise representation of

595   target location – or it is possible that nontargets instead helped sustain fixation at or execute

596   saccades to the target more accurately, which as a result could indirectly make the behavioral

597   responses more accurate? To test this latter possibility, we analyzed the influence of nontargets

598   on eye position accuracy (error distance between the target position and actual eye position) as

599   well as eye position variability (RMSD of actual eye position) at the time point when the target

600   was removed from the screen before the localization response (S2 Fig). If anything, the presence

601   of nontargets actually increased eye position error magnitude and variability, suggesting that

602   nontargets indeed facilitated the representation of target location.

603   Our results reflect the idea that nontargets perform as anchors or landmarks, so that the

604   target localization could be done with them as relative references in space, consistent with

605   previous literature (e.g., [10]; see later discussion on the effect of reference frame). Note that in

606   our experiments, we did not explicitly instruct participants to use nontargets, which means that

607   nontarget information might be processed and used by default, instead of only triggered by

608   instruction. Our results showed that two nontargets facilitated slightly more than one, but the

609   second nontarget did not double the facilitation. A possible reason is that in our design, the two

610   nontargets always appeared inside one rectangle region: they were always on the same side of

611   the target, and their distance to the target was similar (within 1.5° and 2.5° to the target location

612   on the horizontal axis). Thus, the two NT objects might have been grouped together as a single

613   landmark, or simply provided similar information, and therefore, the second nontarget might not

614   have provided much additional reference beyond the first one. We also found that when the

615   initial fixation location and nontargets were on the same side of the target, the presence of

616   nontargets did not add on to the response bias (discussed below in more detail). This result

27

617   supports a similar interpretation, that multiple sources of reference located on the same side

618   might provide some redundant information which is relatively less useful for localization.

619

No additional nontarget facilitation on saccade trials

621   Though nontargets facilitated target localization on both no-saccade and saccade trials,

622   we did not find larger magnitude of NT facilitation on saccade trials compared to no-saccade

623   trials. This means that nontargets did not provide *additional* facilitation across a saccade

624   compared to sustained fixation, consistent across all three experiments. In the visual stability

625   literature, landmarks are often highlighted for their role aiding stability across saccades.

626   However, what is often less emphasized is that these NT effects may occur independently of the

627   saccades. Yet our study is certainly not the first to report this. Deubel and his colleagues showed

628   that a displacement of NT objects following a blank period after the saccade might lead

629   participants to misjudge the target location. When there was no saccade, the displacement of the

630   nontargets after the blank had a similar effect compared to saccade trials, even though during

631   continuous presentation participants could detect target displacement without error [24]. This

632   result pattern was replicated in [12].

633   What does this mean for visual stability? Based on our results as well as previous studies,

634   we propose that nontargets may be useful references during saccades, but the effect of nontargets

635   seems to be more general; i.e., even though saccades pose particular challenges for visual

636   stability, nontargets may not be more helpful in saccade cases than sustained fixation.

637

Bias induced by nontarget location

639   In addition to the nontarget facilitation effect, one of the more interesting influences of

640   nontargets in our study was the biasing of target responses towards the nontarget locations, as

641   well as how this bias interacts with the saccade-related response bias.

642   Response biases between fixation/saccade target and nontarget objects have been shown

643   in previous studies, for example with perisaccadic compression of space [25,26,32] and other

644   types of landmark-related bias [13]. The former paradigm used nontargets that briefly flashed

645   around the time of a saccade, and the latter study tested target localization in the periphery, while

646   our study tested stable nontargets and foveal target localization. We found a similar response

647   bias towards nontarget location as the previous studies, although the magnitude of our nontarget

648   bias was smaller compared with Sheth & Shimojo's result in [13]. This is again likely due to

649   more accurate visual processing in the fovea compared to the periphery.

650   What happened on saccade trials where the saccade-related bias and NT-related bias

651   could both take place? When the nontarget location and the initial fixation were on opposite

652   sides of the target, the nontarget bias combined with (i.e., counteracted) the saccade-related bias.

653   However, we found that when the nontargets and initial fixation were on the same side, the two

654   sources of biases did not appear to combine; in fact, the response bias was not any larger than the

655   saccade-related bias alone (i.e., saccade trials with zero nontargets).

656   This result pattern we found was partially shown in Sheth and Shimojo's study. They

657   found that when a salient landmark was displayed on the opposite side of the fixation to the

658   target, the response bias was reduced compared to on the same side, meaning that the landmark

659   biased responses in the opposite direction and counteracted the foveal bias to the fixation [13].

660   However, in their study when the landmark-related bias and fixation-induced bias were in the

29

661 same direction, the landmark was at least 42° away from the target, which likely did not induce

662 landmark-related bias at all. Our study carefully controlled the distance between nontargets and

663 the target in same-side versus opposite-side conditions to avoid this distance confound, and we

664 still found this discrepancy between same-side and opposite-side conditions.

665   Why did saccade-related bias and NT bias *not* add up in the same-side condition? One

666 possible explanation is that certain mechanisms exist individually or together preventing the

667 response from getting too far away from the memorized target location. For example, other

668 extra-retinal mechanisms for visual stability, e.g., remapping [3,4,48], might contribute to

669 accurate target localization, and visuomotor feedback systems [49] might also contribute to

670 accurate localization. These mechanisms might function to maintain a maximum level of error

671 tolerance, and as a result, they might prevent the total bias from exceeding that threshold. This

672 possibility can also explain why nontargets located on the same side as the initial fixation still

673 facilitated response performance by reducing response variability (as shown by the size of the

674 ellipses in Fig 2), even while they did not further bias responses.

675   Another possibility is that the information about nontargets on the opposite side was

676 utilized so that it counteracted saccade-related bias, but that on the same side was somehow

677 disregarded. As discussed before, this could be because nontargets and the initial fixation

678 location on the same side were grouped together or provided similar/redundant information. In

679 the real world, we often have multiple nontargets which rarely appear only on the same side. We

680 may be able to achieve accurate target localization by incorporating nontarget information from

681 different locations, and/or by selectively utilizing nontargets in locations that can provide non-

682 redundant information and potentially help most with localization.

683

Nontarget locations in different reference frames

In Experiments 2 and 3, we presented nontargets before the saccade was triggered, and manipulated the NT locations to see whether nontargets in different reference frames would have different effects. We found that compared to the Baseline experiment, the Relative condition (same NT location relative to target) showed a similar amount of NT facilitation, while the Absolute condition (same absolute NT location on screen) showed less facilitation, in terms of both error magnitude and response variability. In addition, the nontarget bias was larger in the Relative condition; in the Relative condition, the nontarget bias overcompensated for the saccade-related bias when they were on opposite sides of the target, while in the Absolute condition, the NT bias did not even fully counteract the saccade bias. In general, for both facilitation and bias effects, the reference frame did not change the overall pattern of the results, but rather modulated the pattern seen in the Baseline condition. One interpretation aligned with previous literature is that the critical information for target localization across saccades was already present in the baseline condition: i.e., the relative spatial information between the saccade target and nontargets, at the time right after the saccade target was presented [10,33]. In the Relative condition, this relative spatial information was also preserved across saccades, likely enhancing the influence of the nontargets, whereas in the Absolute condition, this relative spatial information was not maintained, possibly reducing the influence of the nontargets.

The importance of relative spatial information that we found is consistent with Deubel's finding on the effect of nontarget/landmark displacement [10]. In their study, a displacement of the landmarks broke the relative spatial information between landmarks and the target. Under the assumption that the landmarks are typically stable and unchanged, participants therefore tended to report the target to be displaced in the opposite direction. Our results provide converging

31

707   evidence that the relative spatial information between nontargets and the target is important, not

708   only to decide whether the target was displaced or not, but also to recall the specific target

709   location. While it may seem somewhat counterintuitive that landmarks are more influential when

710   they move with the eyes to preserve relative position, rather than remain stable in environmental

711   or absolute coordinates, this idea is also consistent with a related retinotopic benefit

712   phenomenon, such as spatial attention lingering in retinotopic coordinates after a saccade [35],

713   and more precise memory for retinotopic than spatiotopic locations [36,47]. Note that in our

714   study, the peripheral nontargets in the "relative" condition were not strictly retinotopic, since

715   they moved with the saccade target cue rather than the actual eye position. Thus, during the

716   saccade, the retinotopic locations of the NTs were constantly changing, but the critical *relative*

717   spatial location between the target and NTs was maintained.

718   It should be noted that there was a confound in the Absolute experiment that could

719   potentially lead to a weaker NT effect than the other two experiments. As described above, we

720   attempted to control the distance between the nontargets and the target when the initial fixation

721   location and NT location were on the same side versus opposite sides. However, the only way

722   this was possible in the Absolute condition was to vary the initial nontarget-target distance,

723   resulting in an overall greater average distance for Absolute trials. Previous studies have

724   demonstrated that larger distances between nontargets and the target could reduce the influence

725   of nontargets on target localization [10]. Thus, it is possible that the larger average distance in

726   Absolute experiment contributed to the weaker effects. However, even when we looked at trials

727   in which the NT-target distance was restricted to the equivalent "near-near" cases only, there was

728   still greater facilitation for Relative than Absolute conditions, a result indicating an effect of

729   reference frame on top of the distance effect. Moreover, it is worth emphasizing that the

32

730   existence of a distance effect itself is another example of the importance of *relative* distance to

731   the target.

732

Landmarks or distractors?

734   As discussed above, our results showed that the presence of nontargets both decreased

735   response variability and induced response bias. Did the presence of nontargets actually help with

736   or hurt target localization? In our study, overall nontargets facilitated performance; on average

737   the responses were closer to the correct location when nontargets were presented, suggesting that

738   the nontargets served as helpful landmarks. But it is also possible that the nontargets acted as

739   distractors, because the responses were biased with smaller variability, as if participants

740   responded more consistently at a wrong location. A related open question is whether subjects

741   were consciously using the nontargets as landmarks to have a more accurate location in mind,

742   and further, whether the presence of nontargets influenced where participants were perceiving

743   the target to be (perceptual bias), and/or where they were clicking the mouse during the decision

744   phase (response bias).

745   Future studies may investigate more into the above two interpretations, to further our

746   understanding of the internal representation of target location. In addition, future work may

747   manipulate the physical properties (e.g., similarity, salience, location, validity) of multiple

748   independent nontargets, to explore how various types of NT information can be incorporated in

749   different real-world scenarios.

750

Conclusion

751

752   In summary, our experiments showed that the presence of nontargets influenced target

753   localization. This influence seemed to manifest as a general effect on target localization rather

754   than something specific to saccade-related processing. We argue that during a localization task –

755   with or without saccade – the spatial location of the target is memorized along with the relative

756   spatial information between the target and nontargets. This information may be stored in memory

757   to reduce response variability, but the information can be distorted such that it induces a response

758   bias at the same time. If the target localization is done across a saccade, the saccade trajectory

759   (initial fixation location and current eye position) might also be stored as spatial references to

760   potentially benefit and/or bias responses, and pre-saccadic and post-saccadic memories are likely

761   incorporated together. Our representation of the target location is thus influenced by a

762   combination of these factors – perhaps weighed by the most non-redundant information – to

763   produce behavioral responses.

764

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765

767

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768

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927

Supporting information

929   ***S1 Fig. Influence of saccade landing position on (saccade-related) response bias.*** *A) Saccade landing*

930   *position. Data are shown for saccade trials with 0 nontargets. Positive values indicate saccade landing*

931   *positions biased towards the initial fixation location (i.e., undershoot). There was a significant saccade*

932   *undershoot on average when there was zero NT, $t(47)=11.33$, $p<.001$, Cohen's $d=1.635$. B) Saccade-*

933   *related response bias. Here bias (directional errors) is shown for no-saccade and saccade trials with 0*

934   *nontargets. Positive values indicate a response bias towards the initial fixation location on saccade trials,*

935   *and towards right on no-saccade trials. Data here are replotted from main test Figure 4, 0-NT. C)*

936   *Saccade-related response bias in undershoot trials and overshoot trials. The saccade trials in (B) were*

937   *separated into undershoot trials and overshoot trials based on saccade landing position. Again, positive*

938   *values indicate a response bias towards the initial fixation location, and this bias was found in both*

939   *undershot and overshot trials, with only a difference in the magnitude of the bias. The schematic above*

940   *shows the scenarios indicated by the results. Arrows show the direction of saccades; eye symbols indicate*

941   *the saccade landing positions; red crosses indicate the correct target locations; black crosses show the*

942   *actual response locations. This part of data was submitted to 2 (saccade landing position: undershoot,*

943   *overshoot) × 3 (experiment: 1, 2, 3) mixed-design ANOVA. There was a significant main effect of saccade*

944   *landing position, $F(1,45)=9.102$, $p=.004$, $\eta_p^2=.168$, but no interaction between saccade landing position*

945   *and experiment, $F(2,45)=0.035$, $p=.965$, $\eta_p^2=.002$. The response bias was indeed smaller on overshoot*

946   *trials compared to undershoot trials, but it was still significantly greater than zero in each experiment,*

947   *t's≥2.802, p's$\leq.013$, Cohen's d's≥0.700 (p values corrected for multiple comparisons). N=16 for each*

948   *experiment. Error bars are SEM.*

949

950   ***S2 Fig. Influence of nontarget number on eye position.*** *A) Eye position error magnitude defined as the*

951   *distance between the final eye position just before response period and the correct fixation/saccade target*

952   *location, incorporating error on both horizontal and vertical axes. Compare to main text Figure 3A*

953   *(influence of nontarget number on manual target localization response accuracy). Whereas nontargets*

954   *decreased manual target localization error (improving performance), the same pattern was not found for*

955   *eye position (oculomotor) accuracy. A 2 (saccade presence: 0, 1) × 3 (NT number: 0, 1, 2) × 3*

956   *(experiment: 1, 2, 3) mixed-design ANOVA found a significant main effect of NT number, that the*

957   *presence of NT(s) actually increased eye position error, $F(2,90)=11.892$, $p<.001$, $\eta_p^2=.209$. B) Similar to*

958   *A) but on eye position variability, calculated using RMSD. Compared to main text Figure 3B where*

959   *nontargets decreased manual response variability, nontargets significantly increased eye position*

960   *variability, $F(1.357,61.077)=3.690$, $p=.047$, $\eta_p^2=.076$. N=16 for each experiment. Error bars are SEM.*

961

962   ***S3 Fig. Different distance conditions in Absolute experiment compared to Baseline and Relative***

963   ***experiments.*** *A) Schematic showing same-side and opposite-side conditions for Relative and Absolute*

964   *experiments (example here shows rightward saccades). Black cross and black circles indicate initial*

965   *fixation location and initial NT positions; white cross and solid circles indicate final fixation location and*

966   *final NT positions. B) Descriptive scatter plots show the response distribution and the 95% confidence*

967   *ellipse, as in main text Figure 2, but here plotted separate for each distance condition in Absolute*

968   *experiment. Data are collapsed across participants for visualization; N=16 for each experiment.*
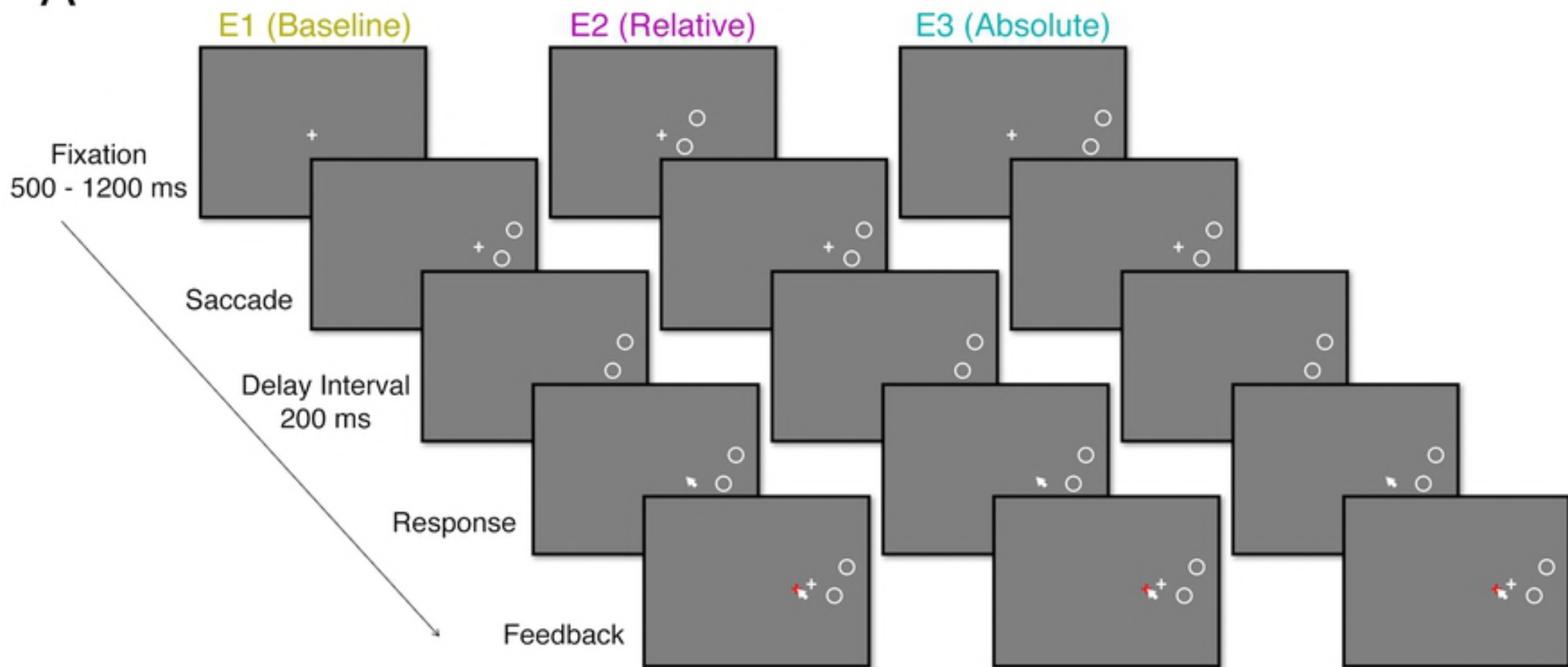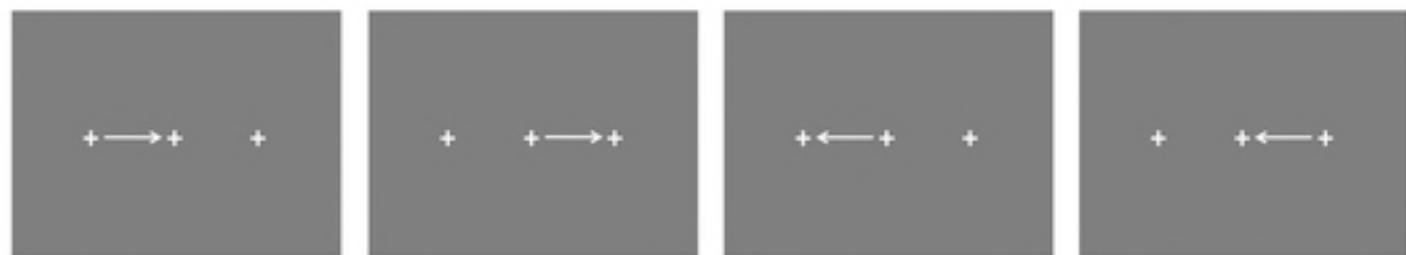
969

970   ***S4 Fig. Influence of different distance conditions on response error magnitude and variability,***

971   ***separating the same- and opposite-side conditions.*** *A) Error magnitude comparisons between three*

972   *distance conditions in Absolute experiment, as well as conditions in the Baseline and Relative*

973   *experiments. Left figure shows opposite-side conditions, and right figure shows same-side conditions. As*

974   *in the main text, we calculated "NT facilitation" as the difference in response error magnitude for 1 and*
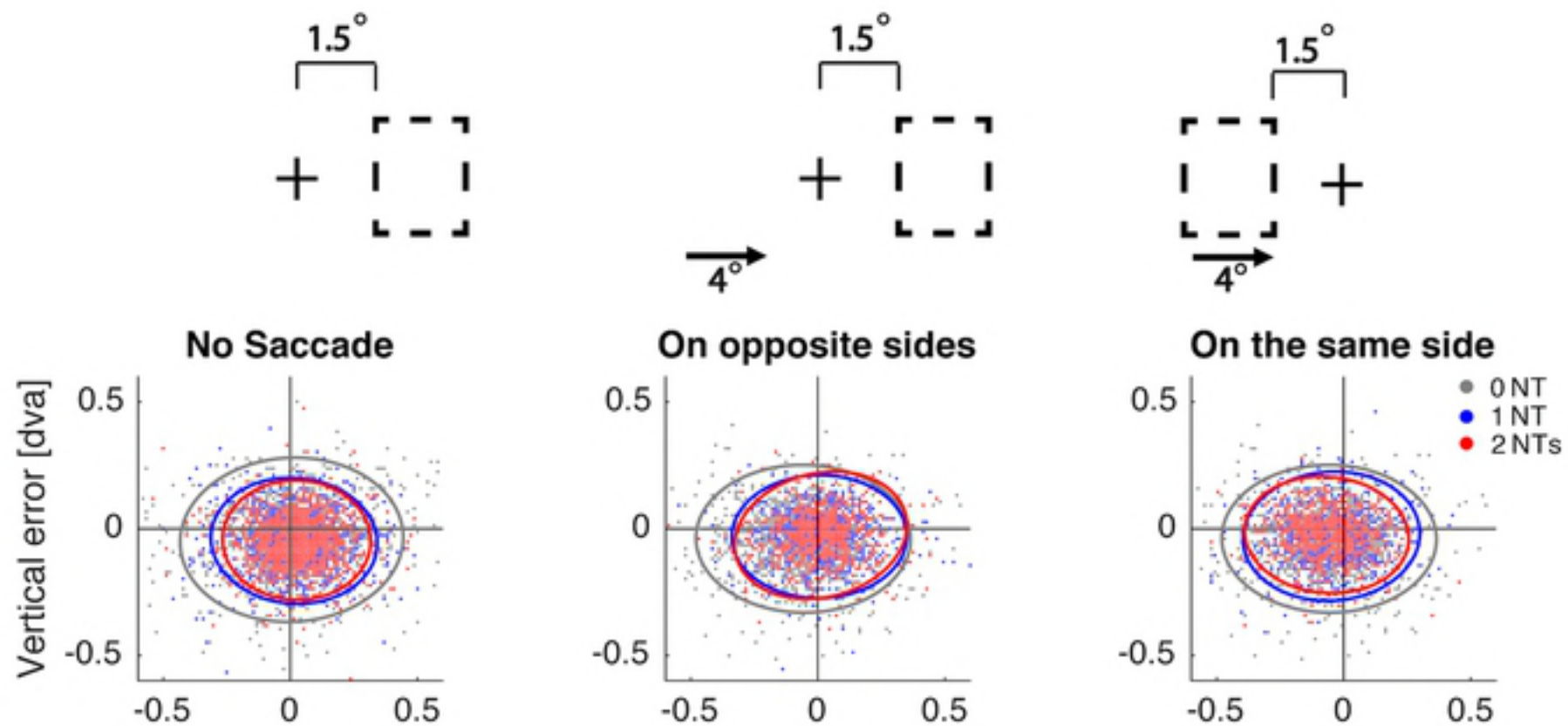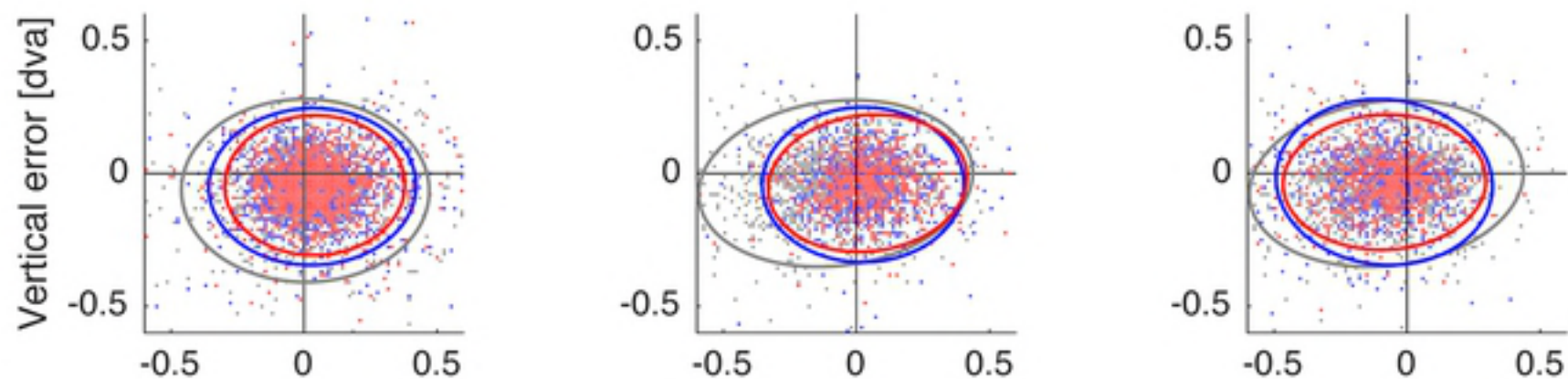
975   *2 NTs compared to the zero NT trials in the same experiment/condition. For the Absolute same-side*

976   *conditions, a 2 (distance: near-far, near-near) × 2 (NT number: 1, 2) mixed-design ANOVA on these*

977   *facilitation scores reported no significant main effects of distance or NT number, nor interaction,*

978   *$F's \leq 2.069$, $p's \geq 171$, $\eta_p^2's \leq 0.121$. There was also no significant difference between absolute-same near-*

979   *near and relative-same (also near-near), $F(1,15)=2.621$, $p=.126$, $\eta_p^2=.149$. B) Similar analyses to A) but*

980   *for response variability. Here there was a significant main effect of distance, $F(1,15)=5.432$, $p=.034$,*

981   *$\eta_p^2=.266$, with stronger facilitation for Abs-same near-near than Abs-same near-far. There was also a*

982   *significant difference between Abs-same near-near and relative-same (near-near), $F(1,15)=10.978$,*

983   *$p=.005$, $\eta_p^2=.423$, revealing an effect of reference frame on top of the distance effect. N=16 for each*
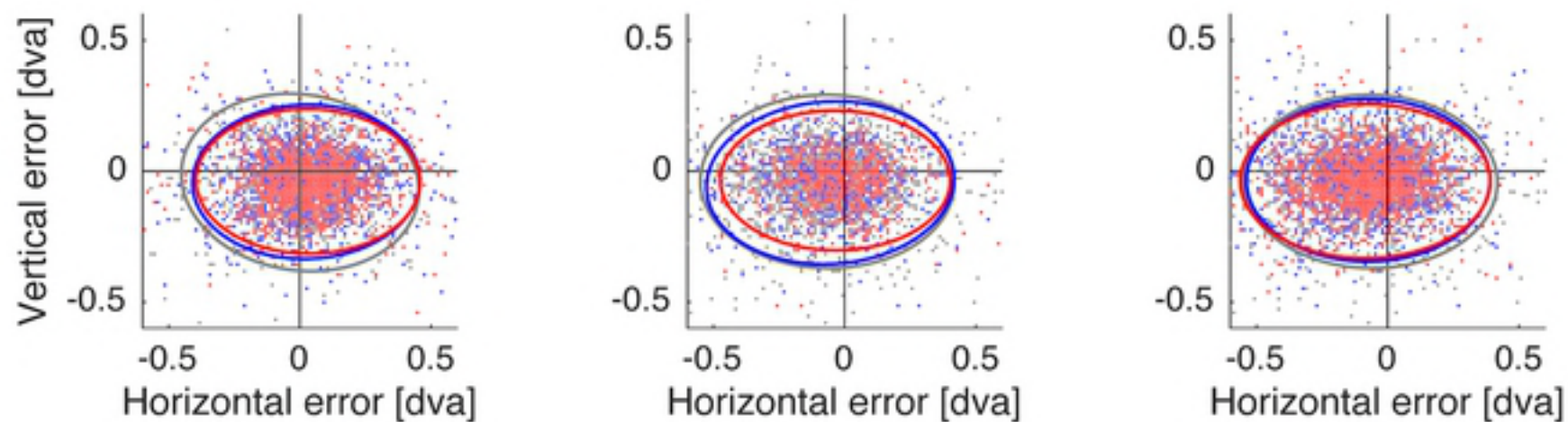
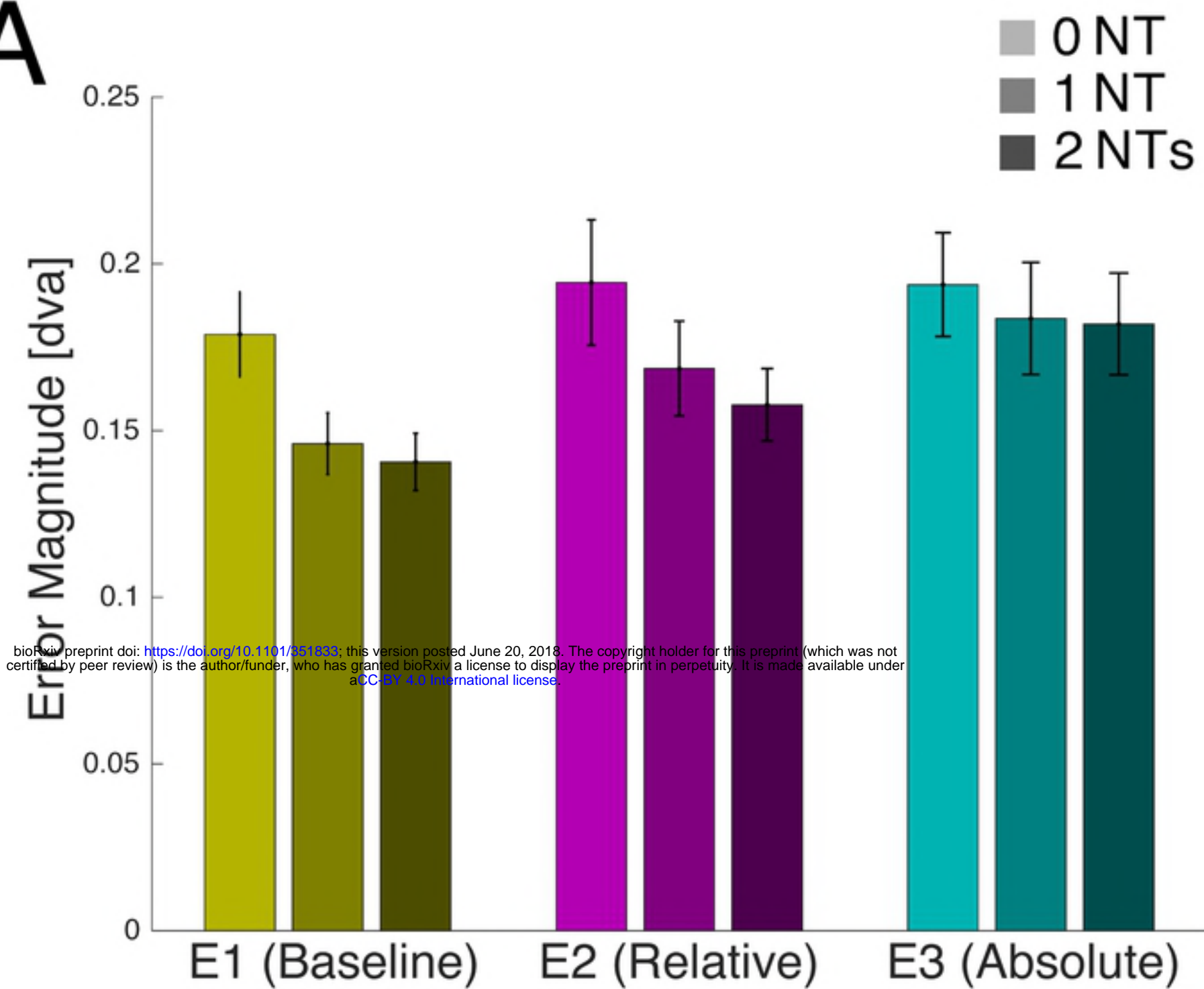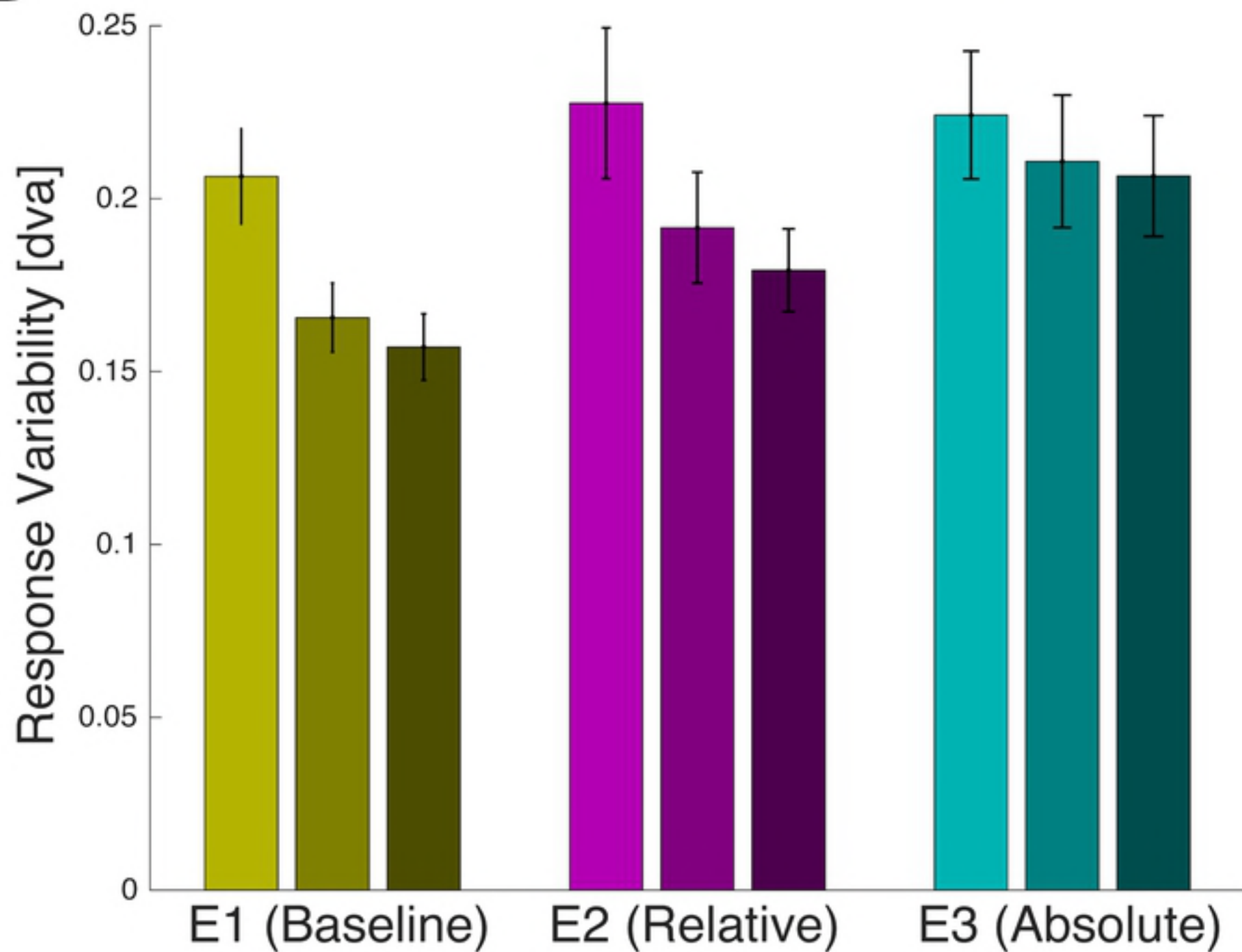984   *experiment. Error bars are SEM.*

A

E1 (Baseline) E2 (Relative) E3 (Absolute)
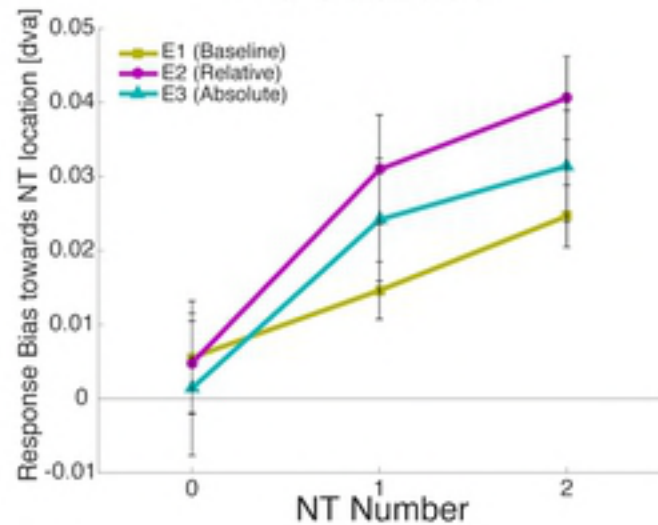
Fixation
500 - 1200 ms

Saccade

Delay Interval
200 ms

Response

Feedback

B

C

A — No Saccade

Response Bias towards NT location [dva] vs NT Number

- E1 (Baseline)
- E2 (Relative)
- E3 (Absolute)

B — On opposite sides

Response Bias towards initial fixation [dva] vs NT Number

C — On the same side

Response Bias towards initial fixation [dva] vs NT Number