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1 2	Inferential Eye Movement Contro	ol while Following Dynamic Gaze
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35	ABSTRACT
36	Attending to other people's gaze is evolutionary important to make inferences about intentions
37	and actions. Gaze influences covert attention and triggers eye movements. However, we know
38	little about how the brain controls the fine-grain dynamics of eye movements during gaze
39	following. Observers followed people's gaze shifts in videos during search and we related the
40	observer eye movement dynamics to the timecourse of gazer head movements extracted by a
41	deep neural network. We show that the observers' brains use information in the visual
42	periphery to execute predictive saccades that anticipate the information in the gazer's head
43	direction by 190-350 ms. The brain simultaneously monitors moment-to-moment changes in
44	the gazer's head velocity to dynamically alter eye movements and re-fixate the gazer (reverse
45	saccades) when the head accelerates before the initiation of the first forward gaze-following
46	saccade. Using saccade-contingent manipulations of the videos, we experimentally show that
47	the reverse saccades are planned concurrently with the first forward gaze-following saccade
48	and have a functional role in reducing subsequent errors fixating on the gaze goal. Together,
49	our findings characterize the inferential and functional nature of the fine-grain eye movement
50	dynamics of social attention.
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72 Introduction

73 Eve movements are involved in almost every daily human activity, from searching for your 74 apartment key, identifying a friend, reading, and preparing a sandwich. People make about 75 three ballistic eye movements (saccades) per second orienting the central part of the vision (the 76 foveola) to regions of interest in the world and acquiring high acuity visual information (Bahill 77 et al., 1975). A foveated visual system allocates more retinal cells and cortical neurons to the central part of the visual field and allows for computational and metabolic savings. But it 78 79 requires that eye movements are programmed intelligently to overcome the deficits of 80 peripheral processing. People execute eye movements effortlessly, rapidly, and automatically 81 giving the impression that these might seem fairly random. However, there are sophisticated 82 computations in the brain that control eve movements involved in fine spatial judgments (Intov 83 & Rucci, 2020; Rucci et al., 2007), search (Araujo et al., 2001; Eckstein et al., 2015; Hoppe & Rothkopf, 2019; Najemnik & Geisler, 2005), object identification (Renninger et al., 2007), face 84 85 recognition (Or et al., 2015; Peterson & Eckstein, 2012), reading (Legge et al., 1997, 2002) and motor actions (Ballard et al., 1995; M. Hayhoe & Ballard, 2005). 86 87 Following the gaze of others (gaze-following) with eve movements is critical to infer others' 88

intentions, current interests, and future actions (Emery, 2000; Kleinke, 1986). Gaze-following 89 90 behavior can be observed as early as 8-10 months in infants and is widely found in nonhumans 91 such as macaques, dogs, and goats (Brooks & Meltzoff, 2005; Kaminski et al., 2005; Senju & 92 Csibra, 2008; Shepherd, 2010; Wallis et al., 2015). The ability to perceive others' gaze direction 93 accurately and plan eye movements is essential for infants to engage in social interactions to 94 learn objects and languages (Carpenter et al., 1998; Morales et al., 1998, 2000; Woodward, 95 2003). People are extremely sensitive to others' direction of gaze (Kleinke, 1986; Langton & 96 Bruce, 1999). When people observe someone's gaze, they orient covert attention and eye 97 movements toward the gazed location, which improves the detection of a target appearing in 98 the gaze direction (Driver et al., 1999; Egeth & Yantis, 1997; Friesen et al., 2004; Han & Eckstein, 99 2022; Jonides & Jonides, 1981; Kingstone et al., 2003; Mulckhuyse & Theeuwes, 2010). Gaze 100 cueing has also been proposed as an important correlate of autism spectrum disorder (Baron-101 Cohen, 2001; Leekam et al., 1998; Nation & Penny, 2008) and important in child development 102 (Brooks & Meltzoff, 2005).

103

104 The majority of studies investigating gaze-following (but see Gregory, 2021; Han & Eckstein,

105 2022; Wang et al., 2014) use static images of the eyes or the face in isolation, which are far

106 from the more ecological real-world behaviors of individuals moving their heads and eyes when

- 107 orienting attention. That gaze cueing triggers eye movements is well known, but the dynamics
- 108 of eye movements when observing gaze behaviors with naturalistic dynamic stimuli are not
- 109 known. Studies have investigated how the brain integrates temporal information to program

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- saccades and how it integrates foveal and peripheral information (Stewart et al., 2020; Wolf et
- al., 2022; Wolf & Schütz, 2015) but have relied on artificial or simplified stimuli.
- 112
- 113 Little is known about what features across the visual field influence eye movements during
- 114 gaze-following, their temporal dynamics, and their functionality. How does the brain rely on the
- features of the gazer's head and peripheral visual information about likely gaze goals to
- program eye movements? Do observers wait for the gazer's head movement to end before
- initiating the first gaze-following saccades? Do visual properties of the gazer's head influence
- 118 the programming of eye movements? Answering these questions has been difficult because
- 119 they require a well-controlled real-world data set, moment-to-moment characterization of the
- 120 gazer's features, and experimental manipulations that alter peripheral information while
- 121 maintaining the gazer's information unaltered.
- 122
- 123 Here, we created a collection of in-house videos of dynamic gaze behaviors in real-world
- settings by instructing actors to direct their gaze to specific people on the filming set (Figure
- 125 1a). We used digital editing tools to erase potential gaze goals while maintaining the gazer's
- 126 movements unaltered and preserving the video's background (Figure 1b-e). We then asked
- 127 experiment participants that watched the videos to follow the gaze shifts in the videos and
- 128 decide whether a specific target person was present or absent (Figure 1a).
- 129
- 130 Our first goal is to assess the impact of peripheral gaze-goal information on the saccade error
- and timing. Second, we aimed to elucidate how the brain temporally processes visual
- 132 information to influence saccade programming during gaze-following. To extract features of the
- 133 videos that we hypothesized would influence saccade planning we used a state-of-the-art
- 134 artificial intelligence (AI) model (Chong et al., 2020) to make moment-to-moment estimates of
- 135 the gazer's head direction in the videos. We assessed how observers' saccade direction, timing,
- and errors related to the extracted features to gain insight into the brain computations during
- 137 saccade planning.
- 138

139 **Results**

140 Integration of peripheral information to guide gaze-following saccades

Twenty-five observers viewed 80 in-house videos (1.2s long, different settings) of an actor (gazer) actively shifting his/her head and gaze to look at another person (gaze-goal) in the video. Participants' initial fixation was on the gazer's head. They were instructed to look where the gazer looks and report whether a specific target person was the gaze goal (Figure 1a). In 25 % of the videos the target person was present and always the gaze goal (Figure 1b). In another 25 %, a distractor person (Figure 1c) was the gaze goal and the target person was absent. In the bioRxiv preprint doi: https://doi.org/10.1101/2022.09.25.508620; this version posted September 27, 2022. The copyright holder for this praprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

- 147 remaining 50%, no person was at the gazed location (d-e). The target/distractor absent videos
- 148 were created by digitally removing the person at the gaze-goal location. The gazers' visual
- 149 information in the videos was identical in the target/distractor present vs. absent videos (Figure
- 150 1b vs. 1d and 1c vs. 1e). Throughout the trial, we measured eye position and detected the onset
- 151 of saccades registered to the video timing. Observers typically executed 3-5 saccades. Figure 1f
- 152 shows a histogram of the number of executed saccades per trial.

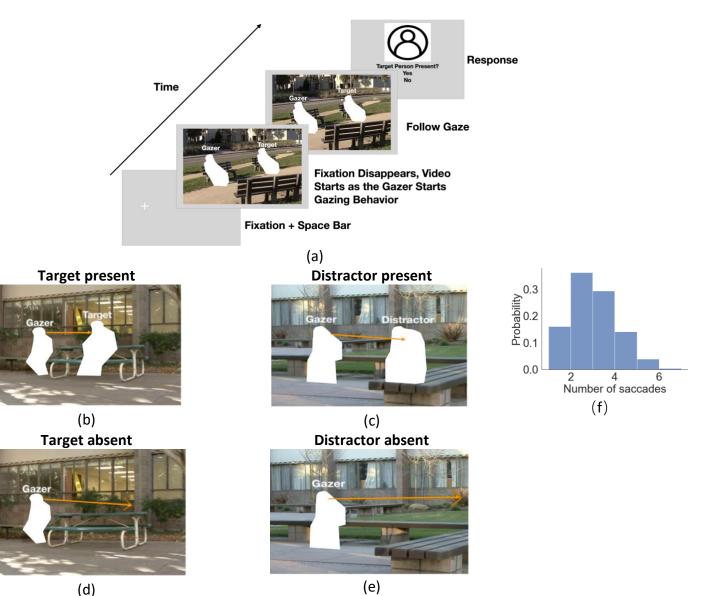


Figure 1. (a) Timeline for each trial. The participants fixated on the fixation cross and pressed the space bar to initialize the trial. The cross was located at the gazer's head, and the trial would not start if the eye fixation moved away from the cross by 1.5°. The cross disappeared as the video started with the gazer starting looking at the designated gazed person (50% present: 25% target and 25% distractor, 50% absent). Participants were instructed to follow the gaze direction and clicked to respond whether the target person was present or not. (b)-(e) Example video frames of the gazer looking at the gaze goal (distractor or target) either with the person present (b,c) or absent

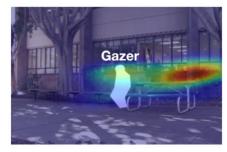
(digitally deleted, d,e). The orange arrow vector is the gaze estimation from a deep neural network model, with details presented in the following section. Note that all the text annotations and arrows are just for illustration purposes and were not presented during experiments. (f) Histogram of the number of saccades participants executed per trial.

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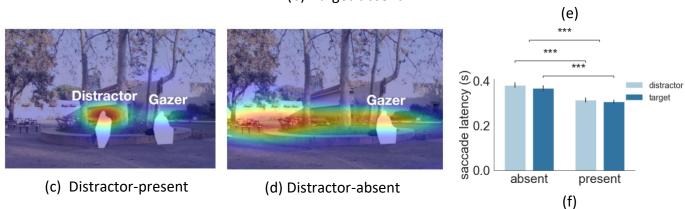
154 To investigate the effect of peripheral information on eye movement planning, we tested the 155 influence of the presence of a person at the gaze goal on the first saccade error and timing. Figure 156 2a-d show heat maps of first saccade endpoint distributions across all observers (for one 157 particular video) and illustrate how the peripheral presence of a person at the gaze goal reduces 158 the error of the first fixation. To quantify the error we calculated the mean Euclidean distance in 159 degrees of visual angle (°) between the saccade endpoint and the center of the gazed person's head. We found that the presence of a person at the gaze goal in the periphery reduced the 160 saccade error (Figure 2e, 2 (present or absent) x 2 (target or distractor) ANOVA, F(1,24)=259, 161 162 p= 2.3e-14). Saccade error was higher when a person was absent vs. present for both target (5.08° vs. 2.50°, p= 1.4e-91, post-hoc paired-test with False Discovery Rate, FDR) and distractor person 163 (5.25° vs. 2.60°, p= 6.8e-106, FDR). The presence of a person at the gaze goal also impacts the 164 165 first saccade latency, (F(1,24)=50.5, p= 2.4e-07). The saccade latency was significantly higher (Figure 2f) when a person was absent vs. present at the gaze goal for both target (0.37s vs. 0.31s, 166 p= 1.4e-16) and distractor (0.38s vs. 0.31s, p= 2.0e-19) trials. There was no difference when the 167 target or distractor person was at the gaze-goal locations neither for first saccade error 168 169 (F(1,24)=1.94, p=0.18) nor first saccade latency (F(1,24)=2.15, p=0.15, Figure 2e-f). 170



(a) Target-present



(b) Target-absent



distractor target

present

saccade error (degree) 0 0 0 b

absent

Figure 2 (a)-(d) Examples of first gaze-following saccade endpoint density maps for target-present. (e) first gaze-following saccade endpoint error. (f) first gaze-following saccade latency.

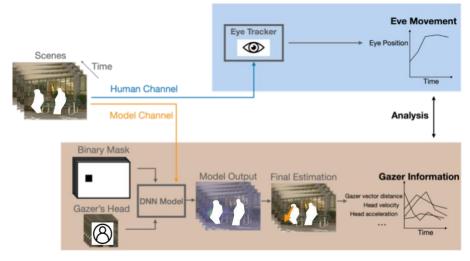
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173 Relating eye movement dynamics to gazer information

174 To relate the dynamics of eye movements (Figure 3a) to the gazer's head information throughout 175 the video, we estimated gaze direction using a state-of-the-art deep neural network (DNN) model 176 (Chong et al., 2020, Figure 3a, see methods for details). The accuracy of the DNN model in estimating the gaze goal location for these images is comparable to that of humans for 177 178 target/distractor present and superior to humans for absent trials (Han et al., 2021). For each 179 video frame, the model generated a gazer vector in which the start point was the gazer's eye 180 position, and the endpoint was the model estimated gaze-goal location. From the frame-to-frame 181 gazer vector, we calculated gazer vector distance in degrees of visual angle (°), angular 182 displacement (deg), head velocity (deg/s), and head acceleration (deg/s²) at a sampling rate of 183 30 frames/sec (see Methods for detailed calculation, see Figure 3b gaze information definitions). We could then relate the observers' saccade execution times to the moment-to-moment changes 184 185 in the gazer vector's measures. We also quantified, from the videos, the typical gazer head 186 velocity before the head stopped. This was accomplished by lining up all videos based on the 187 head stop and averaging the head velocities (Figure 3c).

188



(a)

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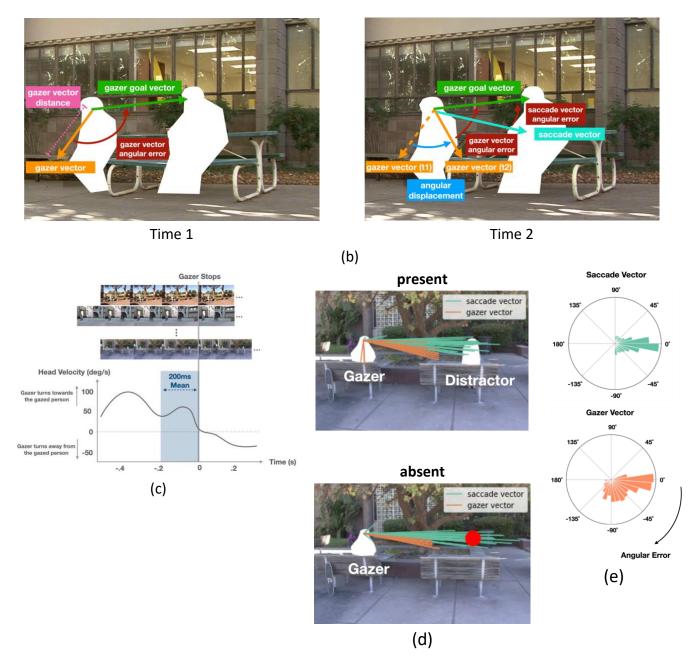


Figure 3. (a). Workflow for AI model for gaze estimation (Chong et al., 2020). The model takes individual frames, paired with a binary mask that indicates the gazer's head location within the scene, and a cropped image of the gazer's head, to produce a probability heatmap. The pixel location with the highest probability was taken as the final estimated gazed location and gazer vector endpoint (orange arrow in final estimation image). We computed various frame-to-frame gaze features based on the gazer vectors and related them to the dynamics of observers' eye movements during gaze-following. (b). Examples of the initial gazer vector, the gazer vector distance, the gazer goal vector, the angular displacement, and angular errors. The gazer vector distance was the vector length indicating how far away the estimated gazed location was from the gazer. The gazer goal vector is the vector whose start point was the gazer's head centroid and the endpoint was the gazer goal location. The angular displacement is the angle between the current gazer vector and the initial gazer vector

position. The *angular error* is the angle between the current *gazer/saccade vector* and the *gazer goal vector*. c) Estimation of the typical head velocities right before (200ms interval) the gazer's head stops moving. Velocities were obtained by aligning all videos with respect to the gaze stop time and averaging the head velocities. Head velocity = 0 at time = 0. (d). The first saccade vectors (teal lines) and corresponding gazer vectors (orange lines) at the saccade initiation times for all observers and trials for the same video (top: present condition, bottom: absent condition). (e). Histogram of angular errors for first saccade vectors and gazer vectors at the saccade initiation times for all trials. All vectors were registered relative to the gazer goal vector (the horizontal direction to the right represents 0 angular error).

189

190 Anticipatory first saccades that predict gaze goal direction

The gazers' head movements started with the video onset and their mean duration was 0.61s. 191 192 The observers' mean first saccade latency was 0.34s (std=0.07s). Thus, the saccade initiation 193 most often preceded the end of the gazer's head movement. In 81% of the trials, participants 194 initiated the first saccade before the gazer's head movement stopped (86% of the trials for target-195 present, 85% for distractor present, and 77% for target/distractor absent trials). We investigated 196 whether these anticipatory first saccades were based on a prediction beyond the available 197 information in the gazer's head direction at the time of saccade initiation. Or on the contrary, are 198 the saccade directions based on the information in the gazer's head direction at the time of 199 saccade initiation?

200

201 To evaluate these hypotheses, we measured the angular error between the DNN-estimated gazer's head direction (gazer vector) at the time of the first saccade initiation and the gazer goal 202 203 vector (Figure 3b right) for each trial. The gazer vector angular error at the time of saccade 204 initiation provides a lower bound on observers' saccade angular error if the brain only used the 205 gazer's head direction to program the eye movements. Figure 3d visualizes the first saccade 206 vectors (teal lines) and corresponding gazer vectors (orange lines) at the saccade initiation times 207 for all observers and trials for a sample video. The results show how the saccade directions are 208 closer to the gazer goal direction than the direction information provided by the gazer's head at the time of saccade initiation (gazer vector). Figure 3e shows co-registered saccade vectors and 209 210 gazer vectors at the time of saccade initiation across all trials/observers. The horizontal line 211 pointing to the right represents zero angular error (i.e., a saccade or gazer vector that points in 212 the same direction as the direction of the gazer goal). The mean angular error for the saccade 213 directions was significantly smaller than that of the gazer vector at the time of saccade initiation 214 (18 degrees vs. 40 degrees, bootstrap p<1e-5). This difference was larger for target/distractor 215 present videos (14 degrees vs. 42 degrees, bootstrap p<1e-5) but was still significant even when 216 the target/distractor was absent (22 degrees vs. 38 degrees, bootstrap p<1e-5). The findings 217 suggest that observers make anticipatory first saccades that infer the direction of the gaze goal 218 beyond the momentary information from the gazer's head direction. We estimated the 219 additional time after saccade initiation it took for the gazer's head to point in the direction of the 220 saccade.On average it took 0.37s (std across observers=0.11s) and 0.22s (std across 221 observers=0.09s) for the gaze vector to reach the saccade vector direction for videos with target/distractor present and target/distractor absent respectively. 222

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223

224 To make sure the results were not due to inadequate gaze estimates by the DNN, we repeated 225 the analysis with humans-estimated gazer vectors instead of DNN-estimated gazer vectors. The 226 human-estimated gazer vectors were obtained from ten individuals (not participants in the study) 227 that viewed randomly sampled individual frames from the videos and were instructed to select 228 the gaze goal (see methods). Because we were interested in measuring the inherent information 229 provided by the gazer's head direction independent of the peripheral information, the 230 participants viewed frames from the target/distractor absent videos. The human-estimated gazer 231 vectors resulted in smaller angular errors than the DNN but showed similar findings. Observers' 232 mean first saccade angular error was significantly smaller than the mean human gazer vector 233 angular error (18 degrees vs. 32 degrees, bootstrap p<1e-5). This effect was present for both, the 234 target/distractor present videos (14 degrees vs. 36 degrees, bootstrap p<1e-5) as well as the 235 target/distractor was absent (22 degrees vs. 27 degrees, bootstrap p=0.017). On average it took 236 0.34s (std=0.12s) and 0.16s (std=0.09s) and for the gazer vector to reach the 1st saccade vector 237 location for the present and absent conditions.

238

239 Frequent reverse saccades triggered by gazer's low head velocity

240 Even if we explicitly instructed participants to follow the gaze, our analysis of eye position 241 revealed that participants executed backward saccades in the opposite direction of the gazer 242 vector (reverse saccades) in 22% of all trials (see Figure 4a for an example). The mean reverse 243 saccade initiation time was 0.63s (std= 0.07s, Figure 4b). Over 80% of the reverse saccades were 244 either the second or the third saccade in the trial (reverse saccade index, Figure 4b). The mean 245 duration of the gazer's head movement during reverse saccade trials was 0.65s. In 87% of the 246 videos, the gazer started to look away from the gazer person at the end of the movie (DNN 247 estimation mean=0.98s, std=0.18s, human estimation mean=1.06s, std=0.15s). In those videos, 248 the majority of reverse saccades (88%) were executed before the gazer started looking away. 249 Figure 4c shows the frequency of first saccades and reverse saccades, as well as the overall head 250 velocity over time. Trials with reverse saccade had significantly shorter first saccade latencies 251 compared to those without reverse saccade (Figure 4d, target/distractor present condition 0.23s 252 vs. 0.34s, p=2.6e-67, absent condition 0.27s vs. 0.40s, p=4.2e-50, both posthoc pairwise 253 comparison with FDR). What could explain the shorter first saccade latencies of trials with reverse 254 saccades? One possible interpretation is that early first saccades are unrelated to the stimulus 255 properties and are generated by stochastic processes internal to the observer. Consequently, 256 when the first saccade is executed too early, a compensatory reverse saccade is subsequently 257 programmed.

258

An alternative possibility is that the observer's early first saccade executions are not random but related to some aspect of the gazer's head movement. To investigate this possibility, we first analyzed the average head velocity over time relative to the timings of the video onset (coincident with the gazer head movement onset) and first saccade execution. The analysis was

202 (concluent with the gazer head movement onset) and hist saccade execution. The analysis wa

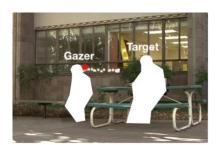
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263 done separately for trials with and without reverse saccade. If the early first saccades in reverse 264 saccade trials are triggered randomly and are unrelated to the gazer's head features, we should 265 find no significant difference in average head velocity between the two types of trials. Instead, 266 we found a significantly lower head velocity during the first 0.23s of the video for the trials with 267 reverse saccades, 63.6 deg/s vs. 93.6 deg/s, cluster-based permutation test, p=1.0e-04 (Figure 268 4e, average head velocity lined up with video start). When we aligned the data with the initiation 269 time of the first saccade, we also observed a significantly lower head velocity for the trials with 270 reverse saccade during 0.37s before the first saccade initiation 47.1deg/s vs. 104.9deg/s, cluster-271 based permutation, p=1.0e-4 (Figure 4f). Furthermore, the average head velocity of 47.1 deg/s 272 was within the range [31.6 deg/s-62.5 deg/s, 95 % confidence interval] of the average head 273 velocity before the gazer's head stops (estimated from all movies; see the horizontal green band 274 in Figure 4e,f). These findings suggest that when the gazer's head velocity is slow, observers make 275 an inference that the gazer might be stopping their head movement. Observers then execute an 276 eye movement to the currently estimated gazer goal. Thus observers' faster first saccades are 277 not executed at random times but are related to the observers' inference that the gazer's head 278 movements might come to a stop. Figure 4f also shows that right before the execution of the first 279 saccade, in reverse saccade trials, the head velocity starts accelerating. We interpret this to 280 indicate that observers infer from the accelerating velocity just prior to the first saccade 281 execution that the gazer's head will not come to a stop. Consequentially, observers program a 282 reverse saccade.



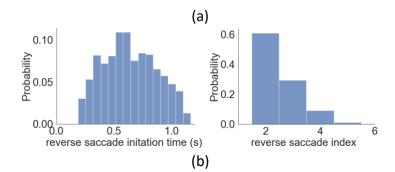


Reverse saccade



Forward saccade (post reverse)





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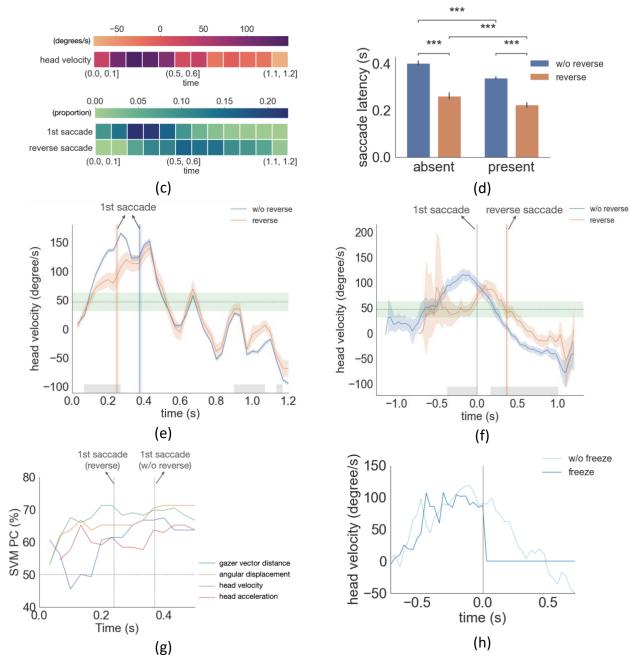


Figure 4. (a) An example of eye movement trace for three saccades over time. A first gazefollowing saccade, followed by a reverse saccade, and another post-reverse saccade gazefollowing saccade. The light red to dark red represents the order in time (see video demo at https://osf.io/yd2nc). (b) Histogram of the reverse saccade initiation time and reverse saccade index (2nd, 3rd, etc.). (c) Heatmaps represent the first saccade and reverse saccade frequency, and the gazer's head velocity over time (d) Saccade latency separated by three conditions and reverse saccade trials. (e) Gazer's head rotation velocity vs. time separated for reverse saccade and non-reverse saccade trials. Shaded areas are the 95% bootstrapped confidence interval. Positive velocity represents moving toward the gazed person's location. The vertical lines are the mean first saccade latency. The gray area shows the statistical significance under the cluster-based permutation test. The green area represents the 95% confidence interval of the velocity right before the gazer's head stops moving across all movies. (f) The same figure as (e) except that head velocity was aligned at the initiation time of the first saccade. (g) The proportion correct of linear SVM models trained to predict whether a movie was in the upper 50 %/or lower 50 % of movies with reverse saccades. The x-axis is the time range from the movie used to train the SVM model. The first saccade latency and reverse saccade latencies are marked as dashed lines as references. (h) The head velocity aligned with the first saccade initiation time at t=0, separately for trials with frozen frames and without.

284

285 Our analysis focused on the head velocity, but what about other features of the gazer's head? 286 The supplementary material S1 shows analyses for other features including distance, angular 287 displacement, and head acceleration. Other features are also significantly different across 288 reverse and non-reverse saccade trials. This is not surprising because there is a correlation 289 between some of the features. For example, before the first saccade execution, the angular 290 displacement is smaller for reverse saccade trials. This is because slower angular velocity for the 291 head will result in lower angular displacement at the time before the first saccade. Still, head 292 velocity showed the clearest results. In order to further investigate whether the head velocity or 293 other gaze features from the videos can better explain reverse saccades, we trained multiple 294 support vector machine (SVM) models using different head features to predict the frequency of 295 reverse saccades (binary prediction: top vs. bottom 50 percentile) using features: 1. Gazer vector 296 distance 2. Angular displacement, 3. Head angular velocity, 4. Head angular acceleration (see 297 Methods for detailed description). We used the time range starting from the beginning of the video and gradually increased the time range for the predictor, and plotted the SVM model 298 299 proportion correct (PC) in Figure 4g. We found that the head velocity had the highest accuracy in 300 predicting reverse saccade movies among all gaze features. The model's accuracy peaked when 301 we used head velocity information from 0-230ms of each video (71.2%) and asymptoted 302 afterward. This was consistent with the results that during the first 0.23s of movies, trials with 303 reverse saccade had a significantly lower head velocity than those without.

304

305 When are the reverse saccades planned?

Having established that the gazer's low head velocity might be triggering an early first saccade in 306 307 trials with reverse saccades, we tried to determine the timing of the reverse saccade 308 programming. One possibility is that the reverse saccades are programmed after the execution 309 of the first forward saccade. In this framework, the gazer's initial slow head velocities in some 310 trials trigger an early first saccade forward and, during that subsequent fixation, the motion of 311 the gazer's head accelerating captures attention and triggers the reverse saccade. A second 312 possibility is that it is the gazer's head velocity increase right before the observer executes the 313 first saccade (Figure 4f) that triggers the programming of the reverse saccade prior to the

314 execution of the first forward saccade. To assess these two hypotheses, we conducted another 315 experiment, in which we monitored in real time the eye position of observers and froze the video 316 frames immediately after participants initiated the first gaze-following saccade (Figure 4h, See 317 demo video at https://osf.io/xpueh). This only occurred randomly in 50 % of the trials to prevent 318 observers from changing their eye movement strategy. If observers' reverse saccades were 319 triggered by the transient motion after the first saccade execution, then freezing the video and 320 eliminating the transient peripheral motion signal of the head should diminish the frequency of 321 the reverse saccades. However, we found that freezing the video frame after the first saccade 322 execution did not reduce the proportion of trials with reverse saccade relative to the unfrozen 323 videos trials, (mean=22%, std=12% for frozen vs. mean=21%, std=11% for unfrozen, bootstrap 324 p=0.6). These results suggest that observers planned the reverse saccade prior to the execution 325 of the first forward saccade.

326

327 Functional role of reverse saccade

Next, we tried to understand the function, if any, of reverse saccades. We first analyzed the 328 329 endpoint of the reverse saccade. We found that the reverse saccades landed close to the gazer's head (Figure 5a; mean distance to the gazer's head 0.79°, std= 0.28°) suggesting that the reverse 330 saccades aim to re-fixate the gazer given the change in the gazer vector after execution of the 331 332 first saccade. To assess the potential functionality of the reverse saccade, we compared the error in fixating the gaze goal (saccade error: saccade endpoint distance to the gazed person's location) 333 of forward saccades before and after the reverse saccade. Figure 5b shows the density map of 334 335 forward saccade endpoints separately for pre and post reverse saccades for a single sample 336 image, as well as the density map combined across all images by registering the saccade 337 endpoints relative to the gazer's head. Forward saccades following a reverse saccade ended 338 closer to the gaze goal than the saccades before reverse saccades. (Figure 5c; 1.8° for post reverse 339 saccade vs. 2.5° for pre reverse, p=0.0054 based on bootstrap resampling, see methods). For the target/distractor absent condition, we did not find this effect, 5.2° vs. 5.3°, p=0.43. Finally, the 340 341 saccade error in the trials without reverse saccades was significantly lower compared to the trials 342 with reverse saccades (present 1.1°, absent 3.7°, all p<0.001, corrected by FDR). This suggests 343 that the gazer information was less ambiguous and more accessible to observers in the trials with 344 no reverse saccades.

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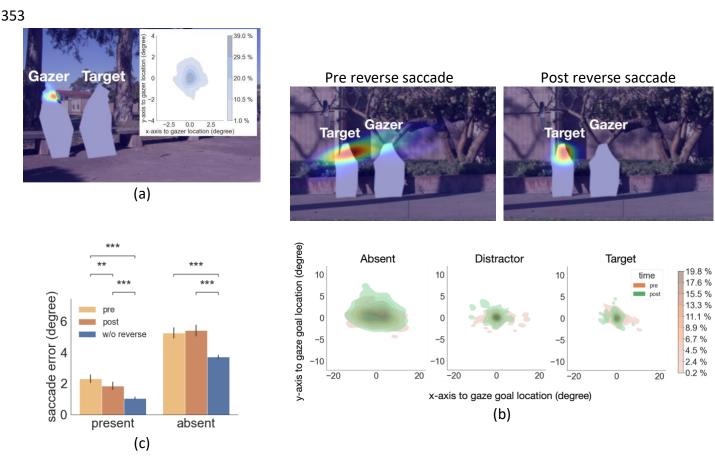


Figure 5. (a) Density map of reverse saccade endpoint locations overlayed an example image. The density map of all reverse saccade locations registered across videos relative to the gazer's head location at origin (0,0) is shown on the top right. Colorbar shows the proportion of saccades falling in each region. (b) Top: Density map of gaze-following saccade location pre- and post-reverse saccade overlaying on an example image. Bottom: Density map of all saccades pre- and post-reverse saccades registered relative to the gazed person's head location at origin (0,0). Colorbar shows the proportion of saccades falling in each region. (c) The saccade error (relative to the gazed location, center of the head) for pre- and post-reverse saccades. Trials with no reverse saccade were treated as the baseline condition.

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356 **Causal influence of re-foveating the gazer with a reverse saccade**

Our analysis showed that the saccade endpoint after the reverse saccade was closer to the gaze goal than the endpoint of the forward saccade preceding the reverse saccade. The interpretation is that re-fixating the gazer with the reverse saccade improved the inference about the gazer goal and benefited the subsequent forward saccade. However, an alternative explanation is that the gaze-following saccade after a reverse saccade simply has longer visual processing compared to the first saccades preceding the reverse saccades (first saccade initiation time m=0.35s vs. first bioRxiv preprint doi: https://doi.org/10.1101/2022.09.25.508620; this version posted September 27, 2022. The copyright holder for this by first (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

363 saccade post reverse saccade initiation time m=0.84s). Longer processing times would result in364 better estimates of the gaze goal.

365

To assess these two competing explanations for the reduction of error of gaze-following saccades after a reverse saccade, we implemented a follow-up experiment with twenty-five new observers. In the new experiment, we digitally erased the gazer on 50 % of the reverse saccade trials (randomly) before the re-fixation of the gazer. To accomplish this, we monitored eye position in real-time, and whenever we detected a reverse saccade during the video, we erased the gazer with a 50 % probability. The experiment allowed comparing the errors of gaze-following saccades subsequent to a reverse saccade with matched visual processing times.

373

374 If the reduced saccade error is related to the foveal re-processing of the gazer after the reverse 375 saccade, we should expect a larger saccade error when we erase the gazer (see Figure 6a 376 example). We first confirmed that the basic analyses replicated the first experiment. The mean 377 reverse saccade initiation time was 0.69s (std = 0.07s), with 80 % of the reverse saccades being 378 the second or the third saccade. Reverse saccades occurred in 31 % of the trials. Trials with 379 reverse saccade had a significantly smaller first saccade latency compared to those without 380 reverse saccade (0.23s vs. 0.33s, bootstrap p<1e-5). Reverse saccade trials were associated with slower head velocity during the initial period of the movie (100ms-260ms) and 150 ms before the 381 first saccade (Supplementary material S2). For trials without the gazer removed, we found the 382 383 same effect of smaller saccade error post reverse saccade for both the present condition (1.4° vs. 1.8°, bootstrap p=1.2e-4) and the absent condition (4.8° vs. 5.2°, bootstrap p=0.04), and (Figure 384 385 6b).

386

387 Critical to our hypotheses testing, the results showed that the saccade error post-reverse saccade was significantly higher in the trials with the gazer removed compared to those with 388 389 unaltered videos, for both the target/distractor present condition (2.5° vs. 1.4°, bootstrap p<1e-5) and the absent condition (5.1° vs. 4.8°, bootstrap p=0.006; Figure 6c). The time of the forward 390 391 saccade following the reverse saccade was the same across trials with the gazer removed or 392 unaltered (0.83s from video onset with the gazer unaltered vs. 0.8s, with the gazer removed, 393 bootstrap p=0.1). This finding confirms that the benefit of reducing the gaze-following saccade 394 errors is causally linked to the uptake of additional gaze goal information from re-fixating the 395 gazer through a reverse saccade.

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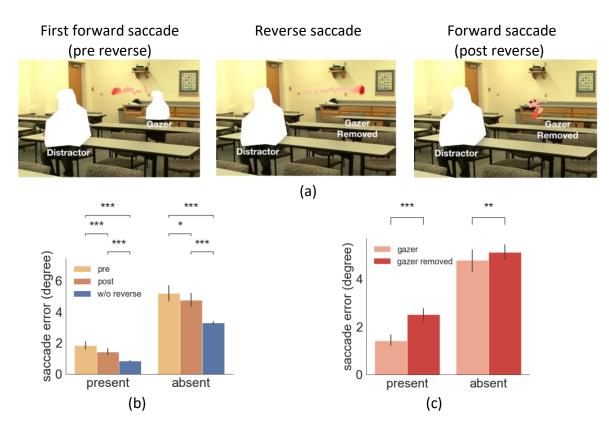


Figure 6 (a) Example of eye movement trace over time when the gazer was erased triggered by a reverse saccade. The light red to dark red represents the order in time (See video demo at https://osf.io/etqbw). (b) The saccade error (relative to gazed person's head) in trials without gazer removed pre reverse saccade vs. post reverse saccade vs. baseline trials (w/o reverse saccades). (c) The saccade error post reverse saccade with gazer removed vs. gazer unaltered.

Anticipatory and reverse saccades during free-viewing search

402 Our two experiments instructed observers to follow the gaze of the person in the video. This 403 might be unnatural, and might have motivated observers to follow the gazer's head movements and trigger anticipatory saccades and reverse saccades. To assess the generality of our findings 404 405 we implemented a control experiment (Experiment 3) with five participants where we did not 406 explicitly instruct observers to follow the gaze during the video presentation. Instead, we only 407 instructed them to evaluate whether they could find the target person and decide whether they 408 were present. No information was given about the gazer or eye movement strategies to follow. 409 We found that participants spontaneously executed gaze-following saccades for 74% (std = 10%) 410 and 91% (std=7.4%) of the trials for the absent and the present condition, respectively (S3). 411 Observers also executed anticipatory first saccades prior to the end of the gazer's head 412 movement on 88% of the trials. We also observed an even larger number of reverse saccades

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413 than in the first experiment where observers were instructed to follow the gazer (33%, std=22%

and 37%, std=16%) of trials for the absent and the target or distractor present condition,

415 respectively). These findings suggest that anticipatory and reverse saccades are not a byproduct

416 of the instructions in experiment 1.

417

418 **Discussion**

419 We investigated eye movement control while following the gaze of others. Although human eye 420 movements are fast and might seem idiosyncratic, our findings show that the human brain uses 421 moment-to-moment information about the gazer's head dynamics and peripheral information 422 about likely gaze goals to rationally plan the timing and endpoint of saccadic eye movements. 423 First, we found that the oculomotor system integrates information about the foveally presented 424 gazer's head and peripheral information about potential gaze goals. When a person was present 425 at the gaze goal, observers executed faster and more accurate saccades. The findings are consistent with a series of studies showing observers' ability to simultaneously process foveal 426 427 and peripheral information for simpler dual tasks with simple stimuli (Ludwig et al., 2014; Stewart 428 et al., 2020) and their joint influence on fixation duration during scene viewing (Laubrock et al., 429 2013) and subsequent eye movements (Wolf et al., 2022). Importantly, the first saccades are 430 anticipatorily initiated before the gazer's head movement comes to a stop. And they contain 431 information about the direction of the gaze goal that is more accurate than the direction 432 information provided by the gazer's head at the time of saccade initiation. This suggests that the 433 brain is using peripheral information to make an active prediction about likely gaze goals. 434 Furthermore, previous studies have shown that a saccade is typically based on visual information 435 presented ~ 80 ms prior to saccade execution (Becker & Jürgens, 1979; Caspi et al., 2004; Hooge 436 & Erkelens, 1999; Ludwig et al., 2005). Thus the first saccade might only have access to the gazer's 437 head direction up to ~80 ms before saccade execution. This inferential process when a person is 438 present in the scene might be expected. But, the finding still prevailed when a target/distractor 439 was absent. It is likely that even when no person is present at the gaze goal location, the brain 440 uses information about the scene including the ground, the objects, and the sky to make 441 estimates of likely gaze goals. Prior knowledge about the maximum angular rotation of the 442 gazer's head also constrains the possible gazer goals.

443

Second, we found that early first saccades are executed when the gazer's head velocity diminishes to values comparable to the velocity that is typical during the 200 ms time interval before the head stops. This is consistent with the idea that observers are using the gazer's head velocity to dynamically make inferences about the likelihood that the head will stop. However, our data also suggest that other cues are used to infer that the gazer's head will stop. For example, for some trials with longer first saccade latencies (no reverse saccade trials), the head velocity 450 before the saccade execution is almost double the typical head velocities during the 200 ms time 451 interval before a head stops (Figure 4e). Thus, the observers must rely on other cues. In these 452 long latency trials (Figure 4e) there is a reduction of the head velocity in the 200 ms before the 453 saccade execution suggesting that observers use the head's deceleration to infer that the gazer's 454 head will come to a stop and then execute the first gaze-following saccade. It is also likely that 455 for trials with a gaze goal, observers use an estimated error between the implied gaze direction 456 and the gaze-goal to plan saccades. Small estimated angular errors might be used to trigger 457 saccades. Thus, we suggest that the oculomotor system might use multiple cues (head velocity, 458 head deceleration, estimated gaze errors, etc) to trigger gaze-following saccades.

459

460 Third, surprisingly, we found that observers often executed reverse saccades in a significant 461 proportion of trials (> 20 %). The reverse saccades were not an artifact of our instruction to the 462 observers to follow the gaze of the person in the video. A follow-up experiment where observers 463 were instructed to decide whether a target person was present with no instruction about eve 464 movements also resulted in a comparable proportion of reverse saccades. Why might observers 465 make such saccades? Our analysis showed that these reverse saccades do not appear randomly 466 across trials. Reverse saccades occur on trials in which the gazer's head velocity is slow but starts 467 accelerating about 200 ms before the first saccade is executed and observers infer that the gazer's head will not come to a halt. Why don't observers simply cancel the forward saccade? 468 469 Studies have shown that there is an 80-120 ms delay between the programming of a saccade and 470 its execution (Becker & Jürgens, 1979; Caspi et al., 2004; Ludwig et al., 2005). The gazer's head 471 acceleration occurring immediately before the execution of the forward saccade is not used to 472 cancel the impending planned eye movement.

473

474 Our findings with the experiment that freezes the gazer after the first forward saccade suggest 475 that the reverse saccade is programmed prior to the execution of the first forward saccade. This 476 concurrent programming of saccades has been documented for simplified lab experiments 477 (Becker & Jürgens, 1979; Caspi et al., 2004) but not in the context of real-world stimuli and tasks. 478 One alternative explanation we did not explore is that reverse saccades are simply triggered after 479 first forward saccades that do not land on the target/distractor. In this perspective, a forward 480 saccade is executed and when foveal processing determines that the saccade endpoint was far 481 from a likely gaze goal then a reverse saccade is programmed and executed (regardless of the 482 velocity of the gazer's head). Data analysis does not favor this interpretation. In a small percentage of trials (15 % of reverse saccade trials) first saccades landed within 0.5° visual angle 483 484 of the target but these were still followed by reverse saccades. This observation suggests the 485 presence of the close-to-fovea gaze goal was not sufficient to interrupt a reverse saccade 486 programmed prior to the execution of the first forward saccade.

488 Our results also show that the reverse saccades had functional importance as forward saccades 489 after re-fixating the gazer were more accurate at landing close to the gaze goal. The benefit of 490 re-fixating the gazer was more reliable when there was a person present at the gaze goal. When 491 a gaze goal person was absent we found a less reliable re-fixation benefit (not statistically 492 significant in experiment 1 and marginally significant in experiment 2) suggesting that not having 493 a peripheral likely gaze goal can be a bottleneck to the accuracy of saccade endpoints. 494 495 The existence of reverse saccades might seem puzzling. Why does the oculomotor programming 496 system not wait longer until the gazer's head comes to a full stop, then executes the gaze-497 following saccade and avoids programming reverse saccades altogether? Executing anticipatory

eye movements that predict future grasping actions (Mennie et al., 2007; Pelz & Canosa, 2001), the location or motion of a stimulus (Fooken & Spering, 2020; Kowler, 1989, 2011; Kowler et al., 2019) is common for the oculomotor system. Thus, while following the gaze of others the oculomotor system plans anticipatory saccades before the completion of the gazer's head movements that predict the gaze goal. Occasionally, these predictive saccades are premature and the brain rapidly programs a reverse saccade to refixate the gazer and collect further information about the potential gazer goal.

505

506 Are the reverse saccades unique to gaze following? No, humans make reverse saccades in other visual tasks that require maintaining information in working memory, such as copying a color 507 block pattern across two locations (M. Hayhoe & Ballard, 2005; M. M. Hayhoe, 2017; 508 Meghanathan et al., 2019). Most notably during reading humans make frequent reverse saccades 509 510 ("called regressive"). Although one might draw a parallel between reading and gaze-following, 511 our findings highlight important distinctions. Regressive saccades during reading are related to 512 inaccurate eye movements that missed critical words or fixations that are too short to deeply 513 process a word's meaning (Inhoff et al., 2019; Rayner, 1998). The reverse saccades while 514 following dynamic gaze are related to moment-to-moment changes in the visual information in 515 the world (i.e. the gazer's head velocity) and the oculomotor systems' rapid strategy changes to 516 optimize gaze-following.

517

518 What might be the brain areas involved in the oculomotor programs for gaze following? There is 519 a large literature relating gaze position to neuronal response properties in the superior temporal 520 sulcus (Oram & Perrett, 1994) and dorsal prefrontal cortex (Lanzilotto et al., 2017). These areas 521 relay information to the attention and gaze network in the parietal and frontal cortex which are 522 responsible for covert attention and eye movements (Pierrot-Deseilligny et al., 2004). Finally, the 523 concurrent programming of saccades has been related to neurons in the Frontal Eye Fields (FEF, 524 (Basu & Murthy, 2020)). Identifying brain areas that integrate peripheral information to generate 525 predictions of likely gaze goals is an important future goal of research.

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526

- 527 One possible limitation of our study is that it focused on the head movement while a large
- 528 literature focuses on the influences of the gazer's eyes (Driver et al., 1999; Friesen et al., 2004;
- 529 Langton et al., 2000; Mansfield et al., 2003; Ristic et al., 2002). Our study was relevant to gazers
- 530 situated at a distance from the observers. The mean angle subtended by the heads in our
- 531 videos (1.47°, std= 0.32°) would match the angle subtended by a real-sized head viewed at a
- 532 distance of 9.3 m (std= 2.0 m) in real life. At that distance, the eye subtends a mean angle of
- 533 0.147° (vertically) providing a poor source of information to infer the gaze goals compared to
- 534 the head orientation. Future studies should investigate gazers at smaller distances from the
- 535 observer and assess how dynamic gazer eye and head movements are integrated and their
- 536 interactions (for static images see Balsdon & Clifford, 2018; Cline, 1967; Langton, 2000; Langton
- et al., 2004; Otsuka, 2014). Similarly, we did not analyze lower body movements. Recent studies
- 538 have shown the diminished influence of the lower body on the orienting of attention (Han &
- 539 Eckstein, 2022; Pi et al., 2020).
- 540

To conclude, our findings reveal the fine-grained dynamics of eye movements while following gaze and the inferential processes the brain uses to predict gaze goals and rapidly program saccades. Given that attending to the gaze of others is an integral part of a normal functioning social attention system, our findings might provide new granular analyses of eye movement control to assess groups with social attention deficits for which simpler gaze following analyses have shown disparate results (Chawarska et al., 2003; Nation & Penny, 2008; Ristic et al., 2005).

548 Materials and Methods

- 549 Experiment 1
- 550 Subjects
- 551 Experiment protocols were approved by the University of California Internal Review Board.
- 552 Twenty-five undergraduate students (ages 18-20, 16 females, 9 males) from the University of
- 553 California Santa Barbara were recruited as subjects for credits in this experiment. All have
- normal to corrected-to-normal vision. All participants signed consent forms to participate in the
- 555 study.
- 556

557 Experimental setup and stimuli

- All videos were presented at the center of a Barco MDRC 1119 monitor with 1280 × 1024
- resolution, subtending a visual angle of 18.4° x 13.8° (width x height). Participants' eyes were
- 560 75cm from the computer screen with the head positioned on a chin rest while watching the
- 561 videos (0.023° visual angle/pixel). Each subject's left eye was tracked by a video-based eye
- tracker (SR Research Eyelink 1000 plus Desktop Mount) with a sampling rate of 1000Hz.

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Subjects' eve movements were calibrated and validated before the experiment. Any large eve 563

drifts that caused failure in maintaining fixation at the beginning of each trial (> 1.5° visual 564

- 565 angle) would result in observers having to do a recalibration and revalidation. Events in which
- velocity was higher than 35°/s and acceleration exceeded 9500°/s² were recorded as saccades. 566 567
- 568 Stimuli consisted of 80 videos (1.2s long) originally taken from videos recorded at the University 569 of California Santa Barbara campus in different settings (classrooms, campus outdoors, student
- 570 apartments, etc.). During the filming, we gave verbal instructions to the actor to look toward
- 571 another person. Once the video starts, one gazer initiated the gazing behavior (looking at
- 572 another person) toward either a distractor person (50% chance) or a target person (50%
- 573 chance). The mean eccentricity of the gazed person relative to the gazer was 6°, std=3°, with a
- 574 minimum of 1.3° and a maximum of 13.6° (Supplementary material S4). The gazed person was
- 575 either present in the video (original) or was erased from the video and appeared invisible.
- 576 Therefore, in total there were 80 videos x 2 (present vs. absent) = 160 video stimuli. To erase
- 577 the gazed individuals from the images, we replaced the RGB values of pixels contained by the
- 578 individual outline (annotated by research assistants) with the RGB values of those pixels of the
- 579 immediate background (Figure 1a-b). The gazed person's location relative to the gazer's head 580 had a mean of 6° visual angle, std=3° visual angle (Figure 1c).
- 581
- 582 Across all the movies, the head regions subtended a mean size of 1.47° (std=0.32°). Given that 583 the average vertical length of eyes spans 2.4cm (0.024m) (Bekerman et al., 2014) and the average vertical distance of the head is about 0.24m (Lee et al., 2006), the eye only 584 585 spanned .147° (std=0.032°).
- 586

587 Procedure

- 588 Subjects were asked to follow the gaze direction as precisely as they can. And if the gazer was 589 looking at a person, they were asked to respond if the target was present or absent. Each
- 590 participant finished sixteen practice trials to make sure they followed the instructions to follow
- 591 the gaze. During the practice, participants had unlimited time to familiarize themselves with
- 592 pictures of the target person. The videos in the practice session were different from the actual
- 593 experiment videos.
- 594
- 595 Participants then completed the main experimental sessions after practice trials. During a
- 596 session, observers completed all videos in random order. In total, each observer finished 2
- 597 sessions x 160 trials/session = 320 trials. Participants first finished a nine-point calibration and
- 598 validation. On each trial, the participants were instructed to fixate a cross and press the space
- 599 bar to start the trial. If the eye tracker detected an eye movement away from the fixation cross
- 600 of more than 1.5° visual angle when they pressed the space bar, the trial would not start, and

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601 participants were required to recalibrate and revalidate. The cross was located exactly at the

- location where the gazer's head would appear once the video started, so we can make sure the
- 603 participants were looking straight at the gazer and observing the gazing behavior. During the
- video presentation (1.2s), participants were asked to follow the gaze direction as precisely as
- they can. Once the video ended, the participants used a mouse to click if the target person was
- 606 present or not (Figure 1d).
- 607

608 AI model estimated gaze information

- In order to quantify the gaze information in each video frame, we used a pre-trained deep
- 610 neural network (DNN) based model (Chong et al., 2020), which makes an objective estimate of
- 611 the gaze location for each video (Figure 3a-b). The model takes an entire image, a binary mask
- that defines a bounding box around the gazer's head location, and a cropped image of the
- 613 gazer's head to produce a probability map of where the head's gaze is directed. We defined the
- 614 model gaze estimation as the pixel location corresponding with the highest probability on the
- 615 probability map. We repeated that for all the image frames from the video to obtain gaze
- estimation over time. To estimate the head angular velocity, we first took the difference in
- 617 *angular displacement* for all continuous pairs of frames and smoothed the estimations by
- 618 convolving the differences with a kernel size of 5 frames. Similarly, we calculated the head
- accelerations based on head velocity differences and smoothed them with a kernel size of 5.
- 620

621 Human estimated gaze information

- 622 Besides the AI model, we also recruited ten undergraduate research assistants to manually
- 623 annotate the gazer vectors for all the video frames where the target or distractor was digitally
- 624 erased. We used target/distractor-absent video frames for human annotations because we
- 625 want to use isolated gaze goal direction information based on the gazer head direction without
- 626 influences from peripheral information about potential gaze goals. We presented all the frames
- 627 in random order. Annotators used Matlab to click on each image to draw the estimated gazer
- 628 vector. We calculated the gazer vector angular error for each annotator and report the average
- angular error as the final human estimated gazer vector for each frame.
- 630

631 Forward and Reverse Saccades Detection

We defined a *forward saccade* as an eye movement in which the direction vector had a positive cosine similarity with the *gazer goal vector*. A *reverse saccade* was defined as a saccade vector that happened after a forward saccade and had a negative cosine similarity with the *gazer goal vector*. In addition, the reverse saccade endpoint was defined to be within a 2.5° visual angle from the gazer to differentiate them from corrective saccades that overshoot the gazer goal. A small subset of saccades was directed in the reverse direction because of the overshooting of the bioRxiv preprint doi: https://doi.org/10.1101/2022.09.25.508620; this version posted September 27, 2022. The copyright holder for this data (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

gaze-following saccade. The endpoints of these reverse saccades had a mean of 6.7° distance to
 the gazer's location. These saccades were considered different from reverse saccades to refixate

- 640 the gazer and were not included in the analysis.
- 641

Distribution of gaze information 200 ms before the gazer's head stops

643 In order to compute the general head velocity range before the gazer stops the gaze behaviors,

644 three annotators manually marked the time stamp when the gazer's head stops moving for

each movie independently. We then defined the gazer stops timing as the average time across

- annotators for each movie. Finally, we calculated the mean gazer vector distance, angulardisplacement, head velocity, and head acceleration during the range of 200ms right before the
- 648 gazer's head stops moving as the benchmarks (Figure 3c).
- 649

650 Statistical Analysis

651 We used within-subject ANOVA and t-tests for mean comparisons across different conditions.

652 We also used bootstrap techniques to estimate the statistical significance of variations of

653 saccade error (e.g., trials with reverse saccade vs. trials without reverse saccade) because of the

non-normality of the distributions. To apply the bootstrap test, we sampled 25 participants with

replacement and calculated the corresponding difference between conditions for each sampled

656 subject (a bootstrap sample), and repeated the process 10,000 times. The distribution of

resampled means or mean differences was used to assess statistical significance. All p values
 were corrected using a false discovery rate (FDR) to reduce the probability of making a Type I

- 659 error. We used cluster-based permutation tests to compare the gazer's head velocity between
- 660 trials with reverse saccades and those without reverse saccades. We computed the mean
- difference for each participant individually and permutated for 10,000 times. Based on

662 corrected p values, we acquired time intervals with significant differences. We used Python to

- 663 analyze all the data. For ANOVA tests we used package "pingouin" (Vallat, 2018). For the cluster-
- based permutation test, we used the package "MNE" (Gramfort et al., 2013).
- 665

666 Support Vector Machine (SVM) Models

667 For training SVM models, we first computed the proportion of trials in which observers

668 executed reverse saccades for each movie. The median proportion of trials that included

reverse saccades for all movies was 20 %. We then did a median split of the movies into two

670 groups as a high possibility of the reverse saccade (>20%) vs. a low possibility of the reverse

671 saccade (<20%). Then we trained the SVM models with radial basis function kernel to classify

672 whether a movie had a high probability of triggering reverse saccade or not. We trained leave-

- 673 one-out SVM based on four gazer vector features: 1. Gazer vector distance 2. Gaze angular
- 674 displacement 3. Head angular velocity 4. Head angular acceleration. For training each SVM
- 675 model, we chose one of the four gaze features during a specific time range from the video

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onset as the predictor. We used the package "sklearn" for the training process (Pedregosa et

- 677 al., 2011).
- 678

679 Experiment 1A (random freeze)

680 Subjects

Five undergraduate students (ages from 18-20, 2 male, 3 female) from the University of

682 California Santa Barbara were recruited as subjects for credits in this experiment. All have

normal to corrected-to-normal vision. All participants signed consent forms to participate in the

- 684 study.
- 685
- 686 Experimental Setup and Stimuli

687 We had the same experiment stimuli and setup as experiment 1, except that we detected 688 saccades during the movie presentation. When we detected the first gaze-following saccade,

there was a 50% chance the gazer would be frozen (without movement) for the rest of the movie

- 690 to prevent any motion afterward that could potentially attract reverse saccade.
- 691
- 692 Procedure

693 The procedure was the same as experiment 1. Participants were told to follow the gaze as 694 precisely as they could during the movie presentation. In total, each observer finished 2 sessions 695 x 160 trials/session = 320 trials. And participants were not aware of the random freezing of the 696 video.

- 697
- 698 Experiment 2
- 699 Subjects

700 Twenty-five undergraduate students (ages from 18-20, 10 male, 15 female) from the University

of California Santa Barbara were recruited as subjects for credits in this experiment. All had

normal to corrected-to-normal vision. All participants signed consent forms to participate in the

- 703 study.
- 704
- 705 Experimental Setup and Stimuli

We had the same experiment stimuli and setup as experiment 1, except that we detected reverse

saccade during the movie presentation. When we detected a reverse saccade back to the gazer

after the first gaze-following saccade, there was a 50% chance the gazer would be completely

- rosed for the rest of the movie, to prevent any foveal processing of the gazer.
- 710
- 711

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- 712 Procedure
- 713 The procedure was the same behavioral task as experiment 1. Participants were told to follow
- the gaze as precisely as they could during the movie presentation. And participants were unaware
- 715 of the random erasure of the gazer.
- 716
- 717 Experiment 3 (free-viewing search)
- 718 Subjects
- 719 Five undergraduate students (ages from 18-21, 3 male, 2 female) from the University of
- 720 California Santa Barbara were recruited as subjects for credits in this experiment. All have
- normal to corrected-to-normal vision. All participants signed consent forms to participate in the
- 722 study.
- 723
- 724 Experimental setup and stimuli
- 725 We used the same experiment stimuli and setup as in experiment 1.
- 726
- 727 Procedure
- The procedure was the same as experiment 1, except that we did not instruct participants to
- follow the gaze explicitly. Instead, we asked them to just free-viewing the video and respond
- whether the target person was present or absent. In total, each observer finished 2 sessions x
- 731 160 trials/session = 320 trials.
- 732

733 Competing Interests

- The authors declare that they have no competing interests.
- 735

736 Data Availability

- 737 Video Stimuli and Data that support the findings of this study have been deposited at osf
- 738 <u>https://osf.io/g9bzt/</u>.
- 739

740 Code Availability

- 741 Code to replicate analysis is available at osf: <u>https://osf.io/g9bzt/</u>.
- 742

743 **Contribution**

- 744 NXH and MPE conceived and designed the studies and determined the data analysis. NXH
- 745 implemented the experiment, collected and analyzed the data. NXH and MPE both wrote the
- 746 manuscript. Both authors approved the final version of the manuscript for submission.

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777 References

- Araujo, C., Kowler, E., & Pavel, M. (2001). Eye movements during visual search: The costs of
- choosing the optimal path. *Vision Research*, *41*(25–26), 3613–3625.
- 780 Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye
- 781 movements. Mathematical Biosciences, 24(3), 191–204. https://doi.org/10.1016/0025-
- 782 5564(75)90075-9
- 783 Ballard, D. H., Hayhoe, M. M., & Pelz, J. B. (1995). Memory Representations in Natural Tasks.
- 784 *Journal of Cognitive Neuroscience*, 7(1), 66–80.
- 785 https://doi.org/10.1162/jocn.1995.7.1.66
- 786 Balsdon, T., & Clifford, C. (2018). Task Dependent Effects of Head Orientation on Perceived
- 787 Gaze Direction. *Frontiers in Psychology*, *9*. https://doi.org/10.3389/fpsyg.2018.02491
- 788 Baron-Cohen, S. (2001). *Mindblindness: An essay on autism and theory of mind*. MIT Press.
- 789 Basu, D., & Murthy, A. (2020). Parallel programming of saccades in the macaque frontal eye
- field: Are sequential motor plans coactivated? Journal of Neurophysiology, 123(1), 107–
- 791 119. https://doi.org/10.1152/jn.00545.2018
- 792 Becker, W., & Jürgens, R. (1979). An analysis of the saccadic system by means of double step
- 793 stimuli. *Vision Research*, *19*(9), 967–983. https://doi.org/10.1016/0042-6989(79)90222-
- 794

- 795 Bekerman, I., Gottlieb, P., & Vaiman, M. (2014). Variations in eyeball diameters of the healthy
- 796 adults. Journal of Ophthalmology, 2014, 503645. https://doi.org/10.1155/2014/503645

797	Brooks, R., & Meltzoff, A. N. (2005). The development of gaze following and its relation to
798	language. Developmental Science, 8(6), 535–543. https://doi.org/10.1111/j.1467-
799	7687.2005.00445.x
800	Carpenter, M., Nagell, K., Tomasello, M., Butterworth, G., & Moore, C. (1998). Social Cognition,
801	Joint Attention, and Communicative Competence from 9 to 15 Months of Age.
802	Monographs of the Society for Research in Child Development, 63(4), i–174.
803	https://doi.org/10.2307/1166214
804	Caspi, A., Beutter, B. R., & Eckstein, M. P. (2004). The time course of visual information accrual
805	guiding eye movement decisions. Proceedings of the National Academy of Sciences of
806	the United States of America, 101(35), 13086–13090.
807	https://doi.org/10.1073/pnas.0305329101
808	Chawarska, K., Klin, A., & Volkmar, F. (2003). Automatic attention cueing through eye

- 809 movement in 2-year-old children with autism. *Child Development*, *74*(4), 1108–1122.
- 810 https://doi.org/10.1111/1467-8624.00595
- 811 Chong, E., Wang, Y., Ruiz, N., & Rehg, J. M. (2020). Detecting Attended Visual Targets in Video.
- 812 2020 IEEE/CVF Conference on Computer Vision and Pattern Recognition (CVPR), 5395–
- 813 5405. https://doi.org/10.1109/CVPR42600.2020.00544
- 814 Cline, M. G. (1967). The perception of where a person is looking. *The American Journal of*
- 815 *Psychology*, *80*(1), 41–50.
- 816 Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-cohen, S. (1999). Gaze
- 817 perception triggers reflexive visuospatial orienting. *Visual Cognition*, 509–540.

- 818 Eckstein, M. P., Schoonveld, W., Zhang, S., Mack, S. C., & Akbas, E. (2015). Optimal and human
- 819 eye movements to clustered low value cues to increase decision rewards during search.
- 820 *Vision Research*, *113*, 137–154.
- 821 Egeth, H. E., & Yantis, S. (1997). VISUAL ATTENTION: Control, Representation, and Time Course.
- 822 Annual Review of Psychology, 48(1), 269–297.
- 823 https://doi.org/10.1146/annurev.psych.48.1.269
- 824 Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of social gaze.
- 825 Neuroscience & Biobehavioral Reviews, 24(6), 581–604. https://doi.org/16/S0149-
- 826 7634(00)00025-7
- 827 Fooken, J., & Spering, M. (2020). Eye movements as a readout of sensorimotor decision
- 828 processes. Journal of Neurophysiology, 123(4), 1439–1447.
- 829 https://doi.org/10.1152/jn.00622.2019
- 830 Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by
- 831 nonpredictive gaze. *Psychonomic Bulletin & Review*, *5*(3), 490–495.
- 832 https://doi.org/10.3758/BF03208827
- 833 Friesen, C. K., Ristic, J., & Kingstone, A. (2004). Attentional effects of counterpredictive gaze and
- 834 arrow cues. Journal of Experimental Psychology. Human Perception and Performance,
- 835 30(2), 319–329. https://doi.org/10.1037/0096-1523.30.2.319
- 836 Gramfort, A., Luessi, M., Larson, E., Engemann, D., Strohmeier, D., Brodbeck, C., Goj, R., Jas, M.,
- 837 Brooks, T., Parkkonen, L., & Hämäläinen, M. (2013). MEG and EEG data analysis with
- 838 MNE-Python. *Frontiers in Neuroscience*, 7.
- https://www.frontiersin.org/articles/10.3389/fnins.2013.00267

- 840 Gregory, S. (2021). Investigating facilitatory versus inhibitory effects of dynamic social and non-
- social cues on attention in a realistic space. *Psychological Research*.
- 842 https://doi.org/10.1007/s00426-021-01574-7
- 843 Han, N. X., & Eckstein, M. P. (2022). Gaze-cued shifts of attention and microsaccades are
- 844 sustained for whole bodies but are transient for body parts. *Psychonomic Bulletin &*845 *Review*.
- 846 Han, N. X., Wang, W. Y., & Eckstein, M. P. (2021). Gaze Perception in Humans and CNN-Based

847 Model. *ArXiv:2104.08447* [*Cs*]. http://arxiv.org/abs/2104.08447

848 Hayhoe, M., & Ballard, D. (2005). Eye movements in natural behavior. Trends in Cognitive

849 *Sciences*, *9*(4), 188–194. https://doi.org/16/j.tics.2005.02.009

Hayhoe, M. M. (2017). Vision and Action. *Annual Review of Vision Science*, *3*(1), 389–413.

851 https://doi.org/10.1146/annurev-vision-102016-061437

Hooge, I. T., & Erkelens, C. J. (1999). Peripheral vision and oculomotor control during visual

search. *Vision Research*, *39*(8), 1567–1575.

Hoppe, D., & Rothkopf, C. A. (2019). Multi-step planning of eye movements in visual search.

Scientific Reports, 9(1), 144. https://doi.org/10.1038/s41598-018-37536-0

- 856 Inhoff, A. W., Kim, A., & Radach, R. (2019). Regressions during Reading. *Vision*, *3*(3), 35.
- 857 https://doi.org/10.3390/vision3030035
- 858 Intoy, J., & Rucci, M. (2020). Finely tuned eye movements enhance visual acuity. Nature
- 859 *Communications*, *11*(1), 795. https://doi.org/10.1038/s41467-020-14616-2
- S60 Jonides, J., & Jonides, J. (1981). Voluntary versus automatic control over the mind's eye's
- 861 *movement*.

bioRxiv preprint doi: https://doi.org/10.1101/2022.09.25.508620; this version posted September 27, 2022. The copyright holder for this **pre**print (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

- 862 http://wexler.free.fr/library/files/jonides%20(1981)%20voluntary%20versus%20automa
- tic%20control%20over%20the%20mind's%20eye's%20movements.pdf
- Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, Capra hircus, follow
- gaze direction and use social cues in an object choice task. Animal Behaviour, 69(1), 11–
- 866 18. https://doi.org/10.1016/j.anbehav.2004.05.008
- 867 Kingstone, A., Smilek, D., Ristic, J., Kelland Friesen, C., & Eastwood, J. D. (2003). Attention,
- 868 researchers! It is time to take a look at the real world. *Current Directions in*
- 869 *Psychological Science*, *12*(5), 176–180.
- 870 Kleinke, C. L. (1986). Gaze and eye contact: A research review. *Psychological Bulletin*, 100(1),
- 871 78–100. https://doi.org/10.1037/0033-2909.100.1.78
- 872 Kowler, E. (1989). Cognitive expectations, not habits, control anticipatory smooth oculomotor
- 873 pursuit. Vision Research, 29(9), 1049–1057. https://doi.org/10.1016/0042-
- 874 6989(89)90052-7
- 875 Kowler, E. (2011). Eye movements: The past 25years. *Vision Research*, *51*(13), 1457–1483.
- 876 https://doi.org/10.1016/j.visres.2010.12.014
- 877 Kowler, E., Rubinstein, J. F., Santos, E. M., & Wang, J. (2019). Predictive Smooth Pursuit Eye
- 878 Movements. *Annual Review of Vision Science*, *5*, 223–246.
- 879 https://doi.org/10.1146/annurev-vision-091718-014901
- Langton, S. R. H. (2000). The mutual influence of gaze and head orientation in the analysis of
- social attention direction. The Quarterly Journal of Experimental Psychology Section A,
- 882 53(3), 825–845. https://doi.org/10.1080/713755908

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- Langton, S. R. H., & Bruce, V. (1999). Reflexive Visual Orienting in Response to the Social
- Attention of Others. *Visual Cognition*, *6*(5), 541–567.
- 885 https://doi.org/10.1080/135062899394939
- Langton, S. R. H., Honeyman, H., & Tessler, E. (2004). The influence of head contour and nose
- 887 angle on the perception of eye-gaze direction. Perception & Psychophysics, 66(5), 752–
- 888 771. https://doi.org/10.3758/BF03194970
- Langton, S. R. H., Watt, R. J., & Bruce, V. (2000). Do the eyes have it? Cues to the direction of
- social attention. *Trends in Cognitive Sciences*, 4(2), 50–59.
- 891 https://doi.org/10.1016/S1364-6613(99)01436-9
- Lanzilotto, M., Gerbella, M., Perciavalle, V., & Lucchetti, C. (2017). Neuronal Encoding of Self
- and Others' Head Rotation in the Macaque Dorsal Prefrontal Cortex. *Scientific Reports*,
- 894 7(1), 8571. https://doi.org/10.1038/s41598-017-08936-5
- Laubrock, J., Cajar, A., & Engbert, R. (2013). Control of fixation duration during scene viewing by
- interaction of foveal and peripheral processing. *Journal of Vision*, 13(12), 11.
- 897 https://doi.org/10.1167/13.12.11
- Lee, J.-H., Hwang Shin, S.-J., & Istook, C. L. (2006). Analysis of Human Head Shapes in the United
 States. *International Journal of Human Ecology*, 7(1), 77–83.
- 900 Leekam, S. R., Hunnisett, E., & Moore, C. (1998). Targets and Cues: Gaze-following in Children
- 901 with Autism. The Journal of Child Psychology and Psychiatry and Allied Disciplines, 39(7),
- 902 951–962. https://doi.org/10.1111/1469-7610.00398

903	Legge, G. E.	., Hooven, T. A.	, Klitz, T. S	S., Stephen	Mansfield, J. S.,	. & Ti	jan, B. S. ((2002). Mr.	Chips

- 2002: New insights from an ideal-observer model of reading. *Vision Research*, 42(18),
 2219–2234.
- Legge, G. E., Klitz, T. S., & Tjan, B. S. (1997). Mr. Chips: An ideal-observer model of reading.
- 907 *Psychological Review*, 104(3), 524–553. https://doi.org/10.1037/0033-295X.104.3.524
- 908 Ludwig, C. J. H., Davies, J. R., & Eckstein, M. P. (2014). Foveal analysis and peripheral selection
- 909 during active visual sampling. *Proceedings of the National Academy of Sciences*,
- 910 201313553. https://doi.org/10.1073/pnas.1313553111
- 211 Ludwig, C. J. H., Gilchrist, I. D., McSorley, E., & Baddeley, R. J. (2005). The Temporal Impulse
- 912 Response Underlying Saccadic Decisions. *Journal of Neuroscience*, *25*(43), 9907–9912.
- 913 https://doi.org/10.1523/JNEUROSCI.2197-05.2005
- 914 Mansfield, E., Farroni, T., & Johnson, M. (2003). Does gaze perception facilitate overt orienting?

915 *Visual Cognition, 10*(1), 7–14. https://doi.org/10.1080/713756671

- 916 Meghanathan, R. N., Nikolaev, A. R., & van Leeuwen, C. (2019). Refixation patterns reveal
- 917 memory-encoding strategies in free viewing. Attention, Perception & Psychophysics,
- 918 81(7), 2499–2516. https://doi.org/10.3758/s13414-019-01735-2
- 919 Mennie, N., Hayhoe, M., & Sullivan, B. (2007). Look-ahead fixations: Anticipatory eye
- 920 movements in natural tasks. *Experimental Brain Research. Experimentelle*
- 921 Hirnforschung. Expérimentation Cérébrale, 179(3), 427–442.
- 922 https://doi.org/10.1007/s00221-006-0804-0
- 923 Morales, M., Mundy, P., Delgado, C. E. F., Yale, M., Messinger, D., Neal, R., & Schwartz, H. K.
- 924 (2000). Responding to Joint Attention Across the 6- Through 24-Month Age Period and

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- 925 Early Language Acquisition. Journal of Applied Developmental Psychology, 21(3), 283–
- 926 298. https://doi.org/10.1016/S0193-3973(99)00040-4
- 927 Morales, M., Mundy, P., & Rojas, J. (1998). Following the direction of gaze and language
- 928 development in 6-month-olds. *Infant Behavior and Development*, *21*(2), 373–377.
- 929 https://doi.org/10.1016/S0163-6383(98)90014-5
- 930 Mulckhuyse, M., & Theeuwes, J. (2010). Unconscious attentional orienting to exogenous cues: A
- 931 review of the literature. *Acta Psychologica*, *134*(3), 299–309.
- 932 https://doi.org/10.1016/j.actpsy.2010.03.002
- 933 Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. Nature,
- 934 434(7031), 387–391. https://doi.org/10.1038/nature03390
- 935 Nation, K., & Penny, S. (2008). Sensitivity to eye gaze in autism: Is it normal? Is it automatic? Is
- 936 it social? *Development and Psychopathology*, 20(1), 79–97.
- 937 https://doi.org/10.1017/S0954579408000047
- 938 Or, C. C.-F., Peterson, M. F., & Eckstein, M. P. (2015). Initial eye movements during face
- 939 identification are optimal and similar across cultures. *Journal of Vision*, *15*(13), 12–12.
- 940 https://doi.org/10.1167/15.13.12
- 941 Oram, M. W., & Perrett, D. I. (1994). Responses of Anterior Superior Temporal Polysensory
- 942 (STPa) Neurons to "Biological Motion" Stimuli. Journal of Cognitive Neuroscience, 6(2),
- 943 99–116. https://doi.org/10.1162/jocn.1994.6.2.99
- 944 Otsuka, Y. (2014). Dual-route model of the effect of head orientation on perceived gaze
- 945 *direction.* Journal of Experimental Psychology: Human Perception and Performance; US:
- 946 American Psychological Association. https://doi.org/10.1037/a0036151

bioRxiv preprint doi: https://doi.org/10.1101/2022.09.25.508620; this version posted September 27, 2022. The copyright holder for this **Afe**print (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

947	Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., Blondel, M.,
948	Prettenhofer, P., Weiss, R., Dubourg, V., Vanderplas, J., Passos, A., Cournapeau, D.,
949	Brucher, M., Perrot, M., & Duchesnay, É. (2011). Scikit-learn: Machine Learning in
950	Python. The Journal of Machine Learning Research, 12(null), 2825–2830.
951	Pelz, J. B., & Canosa, R. (2001). Oculomotor behavior and perceptual strategies in complex
952	tasks. Vision Research, 41(25–26), 3587–3596. https://doi.org/10.1016/s0042-
953	6989(01)00245-0
954	Peterson, M. F., & Eckstein, M. P. (2012). Looking just below the eyes is optimal across face
955	recognition tasks. Proceedings of the National Academy of Sciences of the United States
956	of America, 109(48), E3314-3323. https://doi.org/10.1073/pnas.1214269109
957	Pi, Z., Xu, K., Liu, C., & Yang, J. (2020). Instructor presence in video lectures: Eye gaze matters,
958	but not body orientation. Computers & Education, 144, 103713.
959	https://doi.org/10.1016/j.compedu.2019.103713
960	Pierrot-Deseilligny, C., Milea, D., & Müri, R. M. (2004). Eye movement control by the cerebral
961	cortex. Current Opinion in Neurology, 17(1), 17–25. https://doi.org/10.1097/00019052-
962	200402000-00005
963	Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research.
964	Psychological Bulletin, 124(3), 372–422. https://doi.org/10.1037/0033-2909.124.3.372
965	Renninger, L. W., Verghese, P., & Coughlan, J. (2007). Where to look next? Eye movements
966	reduce local uncertainty. Journal of Vision, 7(3), 6. https://doi.org/10.1167/7.3.6
967	Ristic, J., Friesen, C. K., & Kingstone, A. (2002). Are eyes special? It depends on how you look at
968	it. <i>Psychonomic Bulletin & Review, 9</i> (3), 507–513. https://doi.org/10.3758/bf03196306

bioRxiv preprint doi: https://doi.org/10.1101/2022.09.25.508620; this version posted September 27, 2022. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY 4.0 International license.

969 Ristic, J., Mottron, L., Friesen, C. K., Iarocci, G., Burack, J. A., & Kingstone, A. (2005). Eyes	Eves are
---	----------

- 970 special but not for everyone: The case of autism. *Brain Research. Cognitive Brain*
- 971 *Research*, 24(3), 715–718. https://doi.org/10.1016/j.cogbrainres.2005.02.007
- 972 Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine
- 973 spatial detail. *Nature*, 447(7146), 852–855. https://doi.org/10.1038/nature05866
- 974 Senju, A., & Csibra, G. (2008). Gaze Following in Human Infants Depends on Communicative
- 975 Signals. *Current Biology*, *18*(9), 668–671. https://doi.org/10.1016/j.cub.2008.03.059
- 976 Shepherd, S. V. (2010). Following Gaze: Gaze-Following Behavior as a Window into Social
- 977 Cognition. Frontiers in Integrative Neuroscience, 4.
- 978 https://doi.org/10.3389/fnint.2010.00005
- 979 Stewart, E. E. M., Valsecchi, M., & Schütz, A. C. (2020). A review of interactions between

980 peripheral and foveal vision. *Journal of Vision*, *20*(12), 2.

- 981 https://doi.org/10.1167/jov.20.12.2
- 982 Vallat, R. (2018). Pingouin: Statistics in Python. *Journal of Open Source Software*, *3*(31), 1026.
- 983 https://doi.org/10.21105/joss.01026
- 984 Wallis, L. J., Range, F., Müller, C. A., Serisier, S., Huber, L., & Virányi, Z. (2015). Training for eye

985 contact modulates gaze following in dogs. *Animal Behaviour, 106,* 27–35.

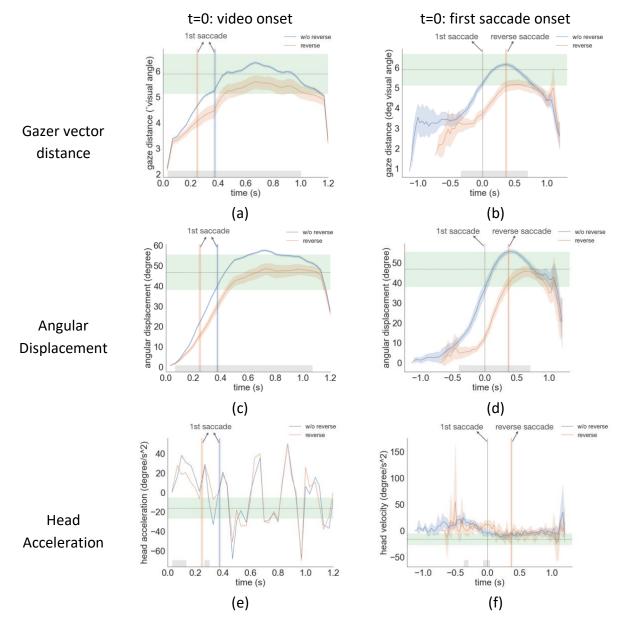
- 986 https://doi.org/10.1016/j.anbehav.2015.04.020
- 987 Wang, L., Yang, X., Shi, J., & Jiang, Y. (2014). The feet have it: Local biological motion cues
- 988 trigger reflexive attentional orienting in the brain. *NeuroImage*, *84*, 217–224.
- 989 https://doi.org/10.1016/j.neuroimage.2013.08.041

990 Wolf, C., Belopolsky, A. V., & Lappe, M. (2022). Current foveal ins

- 991 peripheral preview influence subsequent eye movement decisions. *IScience*, 25(9),
- 992 104922. https://doi.org/10.1016/j.isci.2022.104922
- 993 Wolf, C., & Schütz, A. C. (2015). Trans-saccadic integration of peripheral and foveal feature
- 994 information is close to optimal. *Journal of Vision*, 15(16), 1.
- 995 https://doi.org/10.1167/15.16.1
- 996 Woodward, A. L. (2003). Infants' developing understanding of the link between looker and
- 997 object. Developmental Science, 6(3), 297–311. https://doi.org/10.1111/1467-
- 998 7687.00286

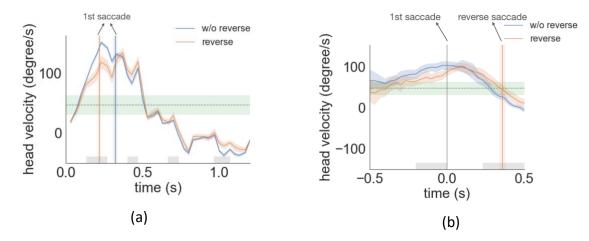
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1021 Supplementary Material

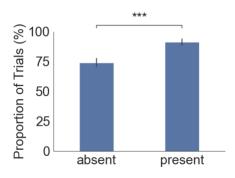


S1. Gazer vector distance, angular displacement, and head acceleration over time, with t=0 aligned with video onset (left column) and t=0 aligned with first saccade onset (right column). The shaded area was the 95% bootstrapped confidence interval. The gray area was significant under the cluster-based permutation test. The green area was the 95% confidence interval of each gaze variable right before the gazer's head stops moving across all movies.

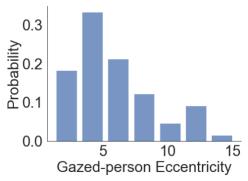
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S2. Gazer's head velocity from the beginning of the movie (a) and aligned with the first saccade initiation time (b) for experiment 2.



S3. The proportion of trials that have the first saccade following the gaze direction for the *absent* and the *present* condition.



S4. The histogram of gazed person eccentricities relative to the gazer's position.