1 **Manuscript Title:**

2 Gaze control during reaching is flexibly modulated to optimize task outcome

3 **Abbreviated Title:**

4 Task demands modulate Eye-hand coordination

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ABSTRACT

When reaching for an object with the hand, the gaze is usually directed at the target. In a laboratory setting, fixation is strongly maintained at the reach target until the reaching is completed, a phenomenon known as "gaze-anchoring". While conventional accounts of such tight eye-hand coordination have often emphasized the internal synergetic linkage between both motor systems, more recent optimal control theories regard motor coordination as the adaptive solution to task requirements. We here investigated to what degree gaze control during reaching is modulated by task demands. We adopted a gaze-anchoring paradigm in which participants had to reach for a target location. During the reach, they additionally had to make a saccadic eye movement to a salient visual cue presented at locations other than the target. We manipulated the task demands by independently changing reward contingencies for saccade reaction time (RT) and reaching accuracy. On average, both saccade RTs and reach error varied systematically with reward condition, with reach accuracy improving when the saccade was delayed. The distribution of the saccade RTs showed two types of eye movements: fast saccades with short RTs, and voluntary saccade with longer RTs. Increased reward for high reach accuracy reduced the probability of fast saccades, but left their latency unchanged. The results suggest that gaze-anchoring acts through a suppression of fast saccades, a mechanism that can be adaptively adjusted to the current task demands.

57   **NEW & NOTEWORTHY**

58   During visually-guided reaching, our eyes usually fixate the target and

59   saccades elsewhere are delayed ("gaze-anchoring"). We here show that the degree of

60   gaze-anchoring is flexibly modulated by the reward contingencies of saccade latency

61   and reach accuracy. Reach error became larger when saccades occurred earlier. These

62   results suggest that early saccades are costly for reaching, and the brain modulates

63   inhibitory online coordination from the hand to the eye system depending on task

64   requirements.

65

66   **INTRODUCTION**

67   When reaching for an object with the hand, gaze is usually directed at the target

68   (see 1, 2, for reviews). One conventional view of eye-hand coordination is that both

69   motor systems share a common control signal for initiating each movement (e.g. 3, 4).

70   Empirical support for this view is that the initiation of hand and eye movement to the

71   target is spatially and temporally coupled (5–9). In other words, eye movements are

72   strongly yoked to movements of the hand by an internal synergetic linkage (10–12). Such

73   strong linkage can be also seen during the execution of a reach. Neggers and Bekkering

74   (13–15) showed that the gaze is locked to the reach target: even when a salient external

75   visual cue is presented, participants seldom initiate saccades until after the hand has

76   reached the target - a phenomenon described as "gaze-anchoring".

77   How fixed is the linkage between hand and eye movements? The framework of

78   optimal control theory (OCT) emphasizes that motor coordination constitutes the

79   adaptive solution to task requirements, rather than resulting from fixed synergetic

80   linkage (16). OCT postulates that characteristics of coordination are determined by how

81   the brain solves the optimal solution for task demands, environments, state of each body

82   effector, and motor effort (17). In other words, coordination patterns should change

83   flexibly to minimize task-dependent cost functions. This theory has succeeded in

84   explaining muscular coordination of limb movements (18–20), the distribution of work

85   across a set of joints for reaching movements (21), and finger coordination for force

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86 production task (22). Optimality in control can not only be found in the flexible

87 distribution of feed-forward motor commands, but also in flexible and task-dependent

88 feedback responses (23, 24). For example, during bimanual reaching movements (25–27),

89 feedback corrections to unpredictable perturbations depend on the nature of the task

90 being achieved with the two hands.

91   In addition to task-dependent coordination of limb movements, several studies

92 also have found flexible changes in eye-hand coordination in well-learned natural tasks

93 (28–30). More critically, two additional studies systematically manipulated task

94 demands, and showed that spatial and temporal eye-hand coordination could indeed be

95 modulated by demands (31, 32). In particular, Sims et al. showed that in a sequential

96 reaching task, the timing of eye movement to the second target relative to the completion

97 of the first reach was adjusted to a nearly optimal solution, which could be predicted by

98 ideal actor model. Similarly, the relative timing between eye and hand movements

99 adapts to the requirement of reaching accuracy (33, 34) and time constraints (35). In all

100 these studies, however, the target for eye movements was kept at the single location

101 across trials and were presented long before the actual movements. In such situation,

102 adaptive coordination patterns could be predetermined before the initiation of each

103 motor action – i.e. the task requirements shape the coordination of feed-forward

104 commands. However, it remains unclear whether the brain adaptively also adjusts eye-

105 hand coordination during online feedback control. Thus, one central claim of OCT,

106 namely that the coordination of both feed-forward and feedback commands is flexibly

107 adjusted according to task-demands, remains untested in the domain of eye-hand

108 coordination.

109   To address this gap, we asked participants to reach and, during on-going

110 movement, to make a saccadic eye movement following an unpredictable shift of the

111 fixation point. We then independently changed the reward schedule for saccade reaction

112 time (RT) and endpoint accuracy of the hand movements. The task allowed us to

113 investigate whether and how eye-hand coupling during on-going reach (i.e. gaze-

114 anchoring) was modulated by reward contingencies.

4

MATERIAL AND METHODS

Participants

Sixteen healthy right-handed naïve participants (7 males, mean age ± SD: 27.3 ± 5.8) gave informed consent to take part in the experiment. The study was approved by the local research ethics committee of the University College London.

Apparatus

Participants made forward reaching movements (20 cm) while holding a planar robotic manipulandum with their right hand (Fig. 1A). Hand position data was recorded at 500 Hz. Visual feedback was provided on a monitor placed above the robot (vertical refresh rate of 60 Hz). This prevented participants from viewing their actual hand/arm. The position of right hand was presented on the monitor by a cursor. Head movements of participants were restricted by a chin-rest where a gaze-tracker was mounted to record gaze position (Eyelink, 500 Hz).

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Figure 1

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Trial procedure

Main task: The trial started when participants put the hand cursor (diameter of 0.3 cm) into the start box and directed the gaze onto to the fixation cross, located 20cm in front of the starting position (Fig. 1A, B). After 500 ms of gaze fixation, a reaching target (square, 1.5 x 1.5 cm) appeared at the same location as the fixation cross, cuing participants to initiate an arm-reaching movement toward the target. On randomly selected trials, the fixation cross shifted to the left or right (7cm along x-axis) when the hand had moved 2cm from the start box in the y-axis direction. Left or right shift occurred with equal probability (i.e. one-third of trials each). The typical timing of reach initiation, fixation shift, and reach termination are shown in Figure 1C. The mean time of fixation shift and reach termination across participants with respect to the reach initiation was 38.9 ± 3.1 ms and 683 ± 15 ms, respectively. In such shift-trials, participants

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145   were asked to make a saccadic eye movement to the new fixation as rapidly as possible

146   while finishing the ongoing reach to the target location. The reaching target (square) was

147   presented at the central location every trial and continued to appear at that place during

148   the trial. In non-shift-trials (remaining one-third of trials), the fixation cross stayed

149   stationary on the target location.

150   The original gaze-anchoring studies (13, 14) adopted a double-step task, where

151   participants started reaching along with the first saccade to the reach target, and then

152   made the second saccade in response to the fixation shift during a reaching. Here, we

153   used a single-step task, where participants could fixate the target long before the

154   movement, and then made a reactive saccade to the fixation shift. We made this

155   methodological change to ensure that the saccadic suppression (36), the saccadic

156   refractory period (37), and/or saccade-related unreliable spatial representation (38–41)

157   would not be able to account for our results.

158   To match reaching behavior across trials, participants were asked to keep peak

159   tangential velocity between 38 - 52 cm/s and movement times between 550 – 800 ms. If

160   those parameters were out of the instructed range, that trial was regarded as failure. In

161   addition, a trial was considered failed if the saccade was executed in the wrong direction,

162   occurred before the shift of the fixation, or was initiated with an extremely short reaction

163   time (< 150 ms). Note that the last criterion was used to exclude false positives caused by

164   head movements or small blinks. The fastest observed saccade RT in the current

165   experimental task was 175 ms. After each trial, participants received feedback about

166   success or failure of that trial. Failed trials were repeated in random order at the end of

167   a conditional block. One condition finished when 30 trials were completed for each

168   fixation shift (rightward, leftward, or non-shift), i.e. each condition consisted of 90

169   successful trials. The failure rate due to the reach- and eye-related criteria was $13.3 \pm 3.7\%$

170   and $1.6 \pm 1.3\%$, respectively.

171   *Saccade only*: In this control task, we examined the RT of saccades without

172   reaching. The trials started when participants put the cursor into the start box, followed

173   by rightward or leftward shift in the fixation cross with a certain delay (1000 ms). In such

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shifted-trials, participants had to make a saccade as fast as possible without moving the hand. In non-shifted trials, participants just maintained gaze fixation for 500 ms. As in the main task, this condition terminated when 90 trials were completed for each saccade directions (leftward, rightward, or non-shift).

Reaching only: In this control task, we examined the effect of a fixation cross shift on reaching behavior without an eye movement. The procedure was the same as in the main task except that participants did not make saccades when the fixation cross moved. As in the main task, this condition terminated when 90 trials were completed for each shift in the fixation cross (leftward, rightward, or non-shift).

Session design

After familiarization with the task and apparatus, participants conducted a Base condition where they were asked to perform the main task as accurately as possible for reaching and as fast as possible for saccade (Fig. 1D). Subsequently, they also performed the main task in reward conditions where they received a reward point (0, 1, or 2) on each trial based on the combination of reach endpoint error (distance from target location) and/or saccade reaction times (RTs). There were three types of reward conditions: (1) only reach accuracy mattered (Hand), (2) only saccade RTs mattered (Eye), or (3) both these measures mattered equally (Both). Participants were instructed explicitly in the beginning of each block regarding the upcoming reward condition. In the Both condition, participants also received a feedback about which motor outputs (saccade RTs or reaching error) they should improve in order to get high reward point on each trial.

We determined thresholds for reward points of each participant based on individual data recorded in the Base condition. In the Hand priority condition, participants won 2 points if reach error was less than the 20th percentile of base-data, won 1 point with error less than the 50th percentile, and 0 points with error more than 50th percentile (leftmost in Fig. 1 E). The same procedure was used for the Eye priority condition by replacing reach error with saccade RTs (rightmost in Fig.1E). Saccade with short RT led to large reward. To keep the overall probability of each reward matched

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204 across conditions, we adjusted the thresholds for the Both priority condition, such that

205 participants won 2 points if both reach error and saccade RT were less than 45th

206 percentile, 1 point with both performance less than 71th percentile, and 0 points with

207 reach error or saccade RT more than 71th percentile (middle in Fig. 1E).

208 Each reward condition (Both, Eye, or Hand) was performed twice, with the

209 order counterbalanced (e.g. Both, Eye, Hand, Hand, Eye, and Both as shown in Fig. 1D).

210 The order of the conditions was varied across participants. To keep participants

211 motivated, thresholds for reward points in the second reward sessions were updated

212 based on the data recorded in the first reward sessions. After all reward sessions, the two

213 control conditions (Saccade only, Reaching only) were conducted (See *Trial procedure* in

214 more detail).

215

216 ***Data analysis***

217 *Reaching movements:* The start of reaching movement was defined as when the

218 hand had moved 1 cm from the stat box in the y-axis direction. The end of the reaching

219 movement was defined as the first time point when the tangential velocity fell below 3.5

220 cm/s for at least 40 ms. The distance between reach endpoint and the target was

221 calculated as the endpoint error for every trial. In the offline analysis, we used not only

222 the endpoint distance error, but also the error in the x-axis (See axis in Fig.1 A), i.e. the

223 error in the direction of the saccade.

224 We are further interested in the effect of saccades on the online reaching

225 trajectory. Thus, we temporally aligned the hand position data in the x-axis with respect

226 to the moment of the shift in the fixation cross. This data was smoothed by Gaussian

227 filter using sigma of 8 ms, and the velocity pattern was calculated by three points

228 numerical time differentiations of filtered data.

229 *Saccadic eye movements:* Saccade initiation was defined as the time at which eye

230 velocity first exceeded 80 °/s. The mean amplitude of the saccade across participants, as

231 determined in offline analyses, was 7.3 ± 0.37 cm.

232 *Session collapsing and trial rejections:* For the reward conditions (i.e. Eye, Hand,

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233   and Both), we collapsed the data across the first and the second reward session, resulting

234   in 60 trials for each saccade direction (leftward, rightward, or non-shift). For the

235   remaining conditions (i.e. Base, Saccade only, and Reaching only), we had 30 trials for

236   each saccade direction. In the offline analysis, we rejected trials in which the saccade

237   amplitude had deviated more than 1.5 times the interquartile range (IQR) from 25th or

238   75th percentile of the data for each participant. This IQR method was also applied to

239   reach endpoint error, reach movement time, and saccade RT for each reward condition.

240   Combined, these criteria led to an exclusion of 9.2%, 7.4%, 7.2%, 9.0%, 4.5%, and 0% of

241   the trials for the Base, Both, Eye, Hand, Saccade only, and Reaching only condition,

242   respectively.

243   *Statistical Analysis:* One-way or two-way repeated ANOVA was used for the

244   statistical test. If the ANOVA was significant, post-hoc test was performed using

245   Ryan's method (42).

246   *Uni-modal vs. Bi-modal saccade RT models:* To examine how the reward condition

247   influenced saccade RTs, we fitted a mixture model to the distribution of saccade RTs.

248   Saccade RTs are known to be right-skewed, following approximately a log-normal

249   Gaussian distribution (e.g. 43) where the logarithm of the RT (x) is normally distributed

250   with a mean of μ and a standard deviation of σ:

251
$$f(x) = \frac{1}{\sigma x \sqrt{2\pi}} exp\left\{-\frac{(\ln x - \mu)^2}{2\sigma^2}\right\} \tag{1}$$

252   However, in the gaze-anchoring task we often observed a bi-modal distribution (see Fig.

253   3A and Appendix Fig. A1). To capture this, we described the distribution using a mixture

254   of two log-normals with a weighting of p_{mix}:

255
$$f(x) = p_{mix}\frac{1}{\sigma_1 x \sqrt{2\pi}} exp\left\{-\frac{(\ln x - \mu_1)^2}{2\sigma_1^2}\right\} + (1 - p_{mix})\frac{1}{\sigma_2 x \sqrt{2\pi}} exp\left\{-\frac{(\ln x - \mu_2)^2}{2\sigma_2^2}\right\} \tag{2}$$

256   We fitted the data with the uni-modal and bi-modal log-normal distribution with Matlab

257   function ("gmdistribution.fit"), and compared models using Bayesian information

258   criterion (BIC):

259
$$BIC = -2\log_e(L) + k\log_e(n) \tag{3}$$

260   where L is the maximized value of the likelihood function, n is the number of data points,

261   and k is the number of parameters ($k=2$ for uni-modal and $k=5$ for bi-modal model).

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262 Model comparison with BIC was performed for each reward condition and each
263 individual separately.

264   *Fixed vs. Flexible bimodal saccade RT models:* The distribution of the saccade RTs
265 across reward conditions (Fig. 3A and Appendix Fig. A1) suggested the idea that the
266 center of fast component of the RT distribution maybe insensitive to reward. The
267 prolongation of mean eye RTs, would then have to be explained by a decreasing
268 probability to make a fast saccade and/or a change in the mean of the second component
269 (i.e. long-RTs trials). To quantitatively test this interpretation, we considered "Fixed-
270 model" where the standard deviation and mean of the first component (σ_1 and μ_1) were
271 kept the same across three reward conditions, and the mixture proportion (p_{mix}) and the
272 parameters for the second component (μ_2 and σ_2) was free to change across conditions
273 (11 free parameters). For the comparison, we considered "Flexible-model" where the
274 parameters (σ_1, σ_2, μ_1, μ_2, and p_{mix}) were flexibly determined for each reward condition,
275 resulting in 15 parameters. For fitting, we minimized the negative log-likelihood across
276 all reward conditions using a nonlinear fitting function in Matlab ("fmincon"). The
277 distribution of the RTs in the Eye condition was nearly uni-modal for many participants,
278 consisting mainly of fast RTs. To ensure that these were captured by the first component,
279 we introduced two constraints for the Eye condition: 1) μ_2 was larger than μ_1 by
280 interquartile range of the distribution, and *2)* p_1 was larger than 0.5. Note that the second
281 constraint was removed for two participants (P4 and P15) whose distribution in the Eye
282 condition was clearly bi-modal with the second component more dominant. Model
283 comparison between "Fixed-model" and "Flexible-model" was conducted with BIC for
284 each participant.

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RESULTS

Saccade reaction times and reaching accuracy

During a reach, the gaze is anchored at the target, which substantially delays saccades elsewhere (13). Gaze anchoring was also observed in the current experiment: The saccade reaction times (RTs) during reaches (Base trials, 434 ± 130.0 ms, [mean ± SD across participants]) were significantly longer than for the Saccade-only trials in the control session (280 ± 30.9 ms, paired t-test, $t(15) = 5.57$, $p < 0.001$). Our aim was to examine whether this feedback-driven eye-hand coordination was flexibly modulated according to reward contingencies.

First, we compared average saccade RTs among reward conditions (Fig. 2A). Saccade RTs for the Hand condition was longer than for other two conditions, indicating that gaze-anchoring was stronger when reaching accuracy mattered. On the other hand, when reward was allocated to the eye movement (i.e. Eye and Both), saccade RTs were markedly reduced. One-way ANOVA revealed a significant main effect of reward condition ($F(2,30) = 23.4$, $p < 0.0001$), and post-hoc test showed a significant difference between the Both and Hand conditions ($t(30) = 5.3$, $p < 0.0001$) and between the Eye and Hand conditions ($t(30) = 6.4$, $p < 0.0001$). These results indicate that gaze-anchoring is not an obligatory feature, but modulated based on reward contingencies. Furthermore, we found that the standard deviation of the saccade amplitude was significantly larger for the Hand condition than other two conditions (Eye vs. Hand: $t(30)=4.11$, $p= 0.0003$, Both vs. Hand: $t(30)=3.33$, $p=0.002$). Placing the reward on reach accuracy not only delayed the saccade but also increased variability of saccade amplitude.

Second, we examined the effect of reward on reaching accuracy. Figure 2B depicts reaching endpoint error, split up by saccade and non-saccade trials. Reaching error changed depending on reward condition and saccade occurrence. A two-way ANOVA (Reward x Saccade) showed a significant main effect of reward condition ($F(2,30) = 9.7$, $p < 0.001$). Post-hoc test showed a significant difference between the Both and Eye condition ($t(30) = 2.79$, $p < 0.01$) and between the Eye and Hand condition ($t(30) = 4.34$, $p < 0.001$), indicating that the reward associated with the reaching aspect (i.e. Both

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320   or Hand) improved reaching accuracy.

321   Reaching accuracy was also influenced significantly by whether or not a saccade

322   occurred during the reach ($F_{(1,15)} = 11.0$, $p < 0.01$). We confirmed that the movement

323   time of the reaching movement for saccade trials was not statistically longer than that

324   for non-saccade trials (one-sided paired t-test, $t_{(47)} = -0.28$, $p = 0.61$). The maximum

325   speed of reaching did not also differ between these trials (one-sided paired t-test, $t_{(47)} =$

326   -3.08, $p = 0.99$). These findings clearly ruled out explanations based on the conventional

327   speed-accuracy tradeoff (44). Rather, our data provides clear evidence that a saccade

328   during the reach negatively influences reach accuracy, and that eye-hand coordination

329   is flexibly modulated according to task demands.

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332   Figure 2

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335   We further examined whether behavioral modulation occurred immediately after

336   the explicitly instructed change in reward condition or whether it gradually developed over

337   the course of a block. To estimate temporal change in behavior, for each reward condition,

338   we averaged reaching error and saccade RTs over every 30 trials and 20 trials (trial block),

339   respectively. A three-way repeated ANOVA with factors of Session (first and second

340   sessions), Trial blocks (three blocks), and Reward conditions (Eye, Both, and Hand) showed

341   no significant effect of Trial block for Reaching error ($F_{(2,30)}=0.52$, $p= 0.60$) or for Saccade

342   RTs ($F_{(2,30)}=0.39$, $p= 0.68$). The interaction of Trial blocks and Reward condition was not also

343   significant for Reaching error ($F_{(4,60)}= 0.65$, $p= 0.63$) or for Saccade RTs ($F_{(4,60)}= 2.05$, $p=$

344   0.10). Thus, neither reaching error nor saccade RTs changed throughout a specific reward

345   condition, suggesting that the change in behaviors was immediate and caused by the explicit

346   instruction at the beginning of the block.

347

348   **Distribution of saccade RTs**

349   What is the mechanism by which the participants delayed their saccade

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especially in the Hand condition? Figure 3A shows the distribution of saccade RTs, plotted separately for each reward condition (2 participants: P13 and P2). The distribution clearly showed a bimodal distribution especially for the Both and Hand conditions. To quantify this observation, we fitted a uni-modal (equation [1]) and bi-modal (equation [2]) log-normal distribution to the data, and compared the quality of the fit using BIC (See Method "*Uni-modal vs. Bi-modal saccade RT models*" for details). For the Hand condition, the bi-modal model provided a better description than the uni-modal model in the majority of participants (13/16 participants), which is statistically significant in a simple Binomial test (p = 0.02). For the eye condition (6/16 better with the bi-modal model) and the Both condition (8/16 better with the bi-modal model), the bi-modality was not as clear in all individual participants.

However, visual inspection of the individual RT distributions (Fig 3A) indicated that the mean of the fast component of the saccade distribution remained the same for the other two conditions. The only thing that appeared to change was the proportion of trials that came from the slower, delayed distribution. To test this idea, we fitted a single bi-modal model across all the individual distribution (See Method *"Fixed vs. Flexible bimodal saccade RT model"* for details.). "Flexible-model" used five free parameters (σ_1, σ_2, μ_1, μ_2, and p_{mix}) for each reward condition. The resultant fits showed that μ_1 was 280 ± 74 ms for the Eye, 302 ± 91 ms for the Both, and 335 ± 138 ms for the Hand condition (mean ± SD across participants). In the comparison between the Eye and Hand conditions, the amount of the change in μ_1 was less than 34 % of the total change in RTs.

On the other hand, the proportion of the first component differed across conditions, and remarkably dropped for the Hand condition (Fig. 3B, "Flexible-model"). In other words, the weight of the second component clearly increased when the reaching accuracy mattered. Indeed, estimated p_{mix} was 0.72 ± 0.27 for the Eye, 0.76 ± 0.24 for the Both, and 0.43 ± 0.28 for the Hand condition (mean ± SD across participants).

To test whether the data could be equally well explained by a fixed first component, we fixed the parameters (μ_1 and σ_1) across the reward conditions ("Fixed model" – the Methods for details). BIC comparison showed that "Fixed-model" was

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379   better than "Flexible-model" in 13 out of 16 participants (Binomial test, p=0.02),

380   indicating that the constraint of fixing the first component explains the individual

381   distribution well. Again, the proportion of the first component (p_{mix}) was the highest for

382   the Eye condition (p_{mix} = 0.81 ± 0.26), and dropped for the Both (p_{mix} = 0.58 ± 0.30) and

383   Hand (p_{mix} = 0.30 ± 0.22) conditions. Anova (F(2,15)=22.2, p < 0.01) and post-hoc test

384   showed a significant difference in the proportion between all the pairs (Eye vs. Both:

385   t(30)=3.0, p < 0.01, Eye vs. Hand: t(30)=6.6, p < 0.01, Both vs. Hand: t(30)=3.6, p < 0.01).

386   Thus, our results suggest that reward contingencies modified saccade behavior by

387   changing the probability of "fast" saccades. Furthermore, the center of "fast" saccades

388   (i.e. μ_1 : 290 ± 74 ms) was not significantly different from the mean saccade RTs for the

389   Saccade-only trials in the control session (280 ± 30.9 ms, paired t-test, t(15) = 0.5, p = 0.62) ,

390   in which participants focused entirely on the saccade without reaching movements. This

391   also suggests that "fast" saccades would be mediated by the fastest visuomotor pathway

392   that could be utilized in the current task.

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394   --------------------

395   Figure 3

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398   **Tradeoff between saccade reaction time and reaching accuracy**

399   Reaching accuracy was clearly modulated not only by reward contingencies but

400   also by whether saccade was made or not (Fig. 2B). This suggests that moving the eyes

401   to a non-target location during a reach has a cost. For a more fine-grained analysis of

402   how saccade RT affected reaching accuracy, we assigned each trial to 1 of 3 bins

403   according to saccade RTs for each reward condition and participant. We then plotted the

404   absolute value of reaching error in the horizontal axis, consistent with the direction of

405   saccade, as a function of saccade RTs for different groups of reward conditions (Fig. 4A).

406   As seen before (Fig. 2A and Fig. 2B), reaching error and saccade RTs generally varied

407   depending on reward contingencies. Furthermore, reaching error for saccade trials was

408   larger than that for non-saccade trials. More interestingly, in each reward condition

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409   (Green, magenta, and blue lines in Fig. 4A), there was a clear tradeoff between reaching

410   accuracy and saccade RTs with trials with longer RTs showing smaller errors. This

411   observation was statistically confirmed by a two-way repeated measures ANOVA

412   (Reward x Bin), which showed a significant main effect of Reward ($F_{(2,30)}$ = 11.07, p =

413   0.0003) and Bin ($F_{(2,30)}$ = 5.76, p = 0.008). A significant interaction did not emerge ($F_{(4,60)}$

414   = 0.62, p = 0.65). These results indicate that the reward condition influenced reaching

415   accuracy in two ways: First, placing a reward on reaching accuracy (Both and Hand

416   conditions) directly reduced the absolute reaching error. This was also supported by the

417   clear decrease in error for those reward conditions in Non-saccade trials (Fig. 4A).

418   Secondly, especially in the hand condition, participants further delayed their saccades,

419   resulting in an additional reduction in reaching error.

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422   Figure 4

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425   **Saccades induced systematic deviations during reaching**

426   To elucidate how saccades influenced the reach, we analyzed the signed

427   endpoint error of reaching in the horizontal axis (x-axis shown in Fig.1A). As shown in

428   Figure 4B, the reach was systematically influenced by the saccade directions. We

429   observed positive error (rightward deviation from the target) when leftward saccade was

430   made, and a leftward deviation when rightward saccade was made. In other words,

431   reaching endpoints tended to be biased to the direction opposite from the saccades (Fig.

432   4B). These findings indicate that saccades induced a deviation of the hand movement in

433   the opposite direction.

434   To further examine why the reaching endpoints were biased in the direction

435   opposite to the saccade, we analyzed online trajectories of reaching movements. We

436   temporally aligned hand velocity signals in the x-axis (x-velocity) with respect to the

437   shift in the fixation cross. We averaged x-velocity of the hand across trials for each

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438   saccade direction, reward condition, and participant. Figure 5A shows averaged hand

439   velocity patterns across participants for different saccade directions under the Both

440   condition. Approximately 300 ms after the fixation cross displacement, the hand

441   movement was deviated rightward for the leftward saccade, and leftward for the

442   rightward saccade. As for the endpoints, the online hand movement was deviated

443   toward the direction opposite to saccades. This finding implies that the endpoint

444   deviation induced by saccades begins immediately after the fixation cross displacement.

445   To quantify the hand response, we computed the difference in the x-hand

446   velocity between saccade directions (leftward – rightward), with larger values denoting

447   larger hand deviation. Figure 5B depicts the mean hand response for three reward

448   conditions (colored curves) and for the Reaching only condition (black dashed curve).

449   The arrow in Figure 5B indicates the mean saccade RTs for each condition. Despite the

450   large difference in saccade RTs among reward conditions, these hand responses for the

451   Eye, Both, and Hand condition initiated at roughly the same time with similar

452   amplitude. In contrast, the response for the Reaching only condition, where participant

453   had to maintain gaze fixation on the original location even when the fixation visually

454   shifted (See Material and Methods for the details), was markedly smaller than for other

455   reward conditions.

456   Based on these observations, one can argue that the lateral hand deviation is

457   triggered by the visual shift of the fixation cross rather than by the execution of the

458   saccades. However, this would be unlikely for two reasons below. Firstly, it is known

459   that reflexive hand responses induced by visual information, such as target shift,

460   background motion, and distractor movements, are directed to the same direction as

461   visual changes (45, 46). Thus, anti-directional response we observed here is difficult to

462   be explained by visually-induced reflexive responses that are generally pro-directional

463   responses. Secondly, the hand response was much smaller when saccade was not made

464   (Reaching only condition). Taken together, we propose that online hand response is

465   probably induced by saccade-related signals during the reaching movement.

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467   --------------------

468   Figure 5

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471

472   **DISCUSSION**

473   We adopted a gaze-anchoring paradigm, and tested whether and how eye-hand

474   coordination is modulated according to task demands. We found clear and systematic

475   changes in saccade RT and reaching accuracy depending on reward contingencies. The

476   analyses of saccade RTs distributions with model approach suggests that the change in

477   gaze-anchoring is achieved by modulating the probability of reflexive and voluntary

478   saccades. We also showed that reach error depended on saccade RTs, with faster

479   saccades leading to larger errors. Our findings show that the brain modulates eye-hand

480   coordination during reaching depending on reward-based task demands.

481

482   **Task-dependent modulation of gaze-anchoring**

483   During a visually-guide reaching, fixating target is strongly favored, which

484   substantially delays saccades elsewhere. This implies that it is mediated by inhibitory

485   coupling from the hand to the eye system. A neurophysiological study suggested the

486   rostral part of superior colliculus, an area classically related to gaze fixation, as a

487   potential neural substrate for gaze-anchoring (47). In contrast to the yoking hypothesis

488   for gaze-anchoring (12–14, 48), under some conditions, participants performed eye

489   movements to the next task-relevant object before the previous actions had been

490   completed (28–30, 49). Importantly, the timing of gaze shift relative to reaching

491   termination adapts to task demands (32–35). In most of those previous studies, however,

492   the targets for hand and eye movements were repeated and predictable. Thus, eye-hand

493   coordination can be pre-planned before the onset of the movement.

494   In our current study we show now clearly that the online coordination between

495   eyes and hand can be modulated in a task-dependent fashion without the need to

496   preplan. Participants did not know the saccade condition (leftward, rightward, or non-

17

497 saccade) before the middle of the reach. While there is neurophysiological evidence that

498 participants likely can preplan eye movement to two potential targets (e.g. Basso and

499 Wurtz 1998), our three target options should have prevented effective pre-planning.

500 Furthermore, we found bimodality of saccade RTs distribution (Fig. 3 and

501 Appendix Fig. A1), suggesting the existence of two types of saccades with different

502 timescales (43, 51). Across reward conditions, the center of "fast" saccade component did

503 not appear to vary. Rather the probability of issuing a "slow", rather than "fast" saccade

504 changed. This suggests that, to modulate gaze-anchoring, the brain did not change the

505 motor commands for "fast" saccades, but modulate inhibitory signals to the generator

506 of "fast" saccades. In particular, when reaching accuracy mattered (Hand), "fast"

507 saccades became less frequently, and were instead replaced by slower, more voluntary

508 saccades. Our results suggest that the brain optimally modulates the strength of

509 inhibitory coupling from the hand to the eye system to make responses to unpredictable

510 visual presentation.

511 Although the "fast" saccades we observed were immutable across reward

512 conditions and appeared to behave like reflexive saccades, they should be considered a

513 different class of eye movements from "express saccade", which occur at very short

514 latencies (human: 80 – 120 ms, monkey: 70 – 80 ms) in the gap-task (e.g. 52). Express

515 saccades are generated through a direct pathway from retina to superior colliculus (e.g.

516 53), and are substantially faster than our "fast" saccades (about 290 ms). Interestingly,

517 Fischer et al. (51) also found three separated peaks in saccade distribution, and called

518 each component, in order of fastest to slowest, "express", "fast regular", and "slow

519 regular" saccades. Thus, the second and third component could correspond to our "fast"

520 and "slow" component. It remains an open question how multiple different cortical

521 saccade pathways may be affected differentially by reward-based task demands.

522

523 **Dependence of reaching accuracy on saccades**

524 Another important aspect of the current study is to explicitly show the

525 dependence of reach accuracy on saccades. First, distance error was significantly larger

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when saccade was accompanied with than when it was not (Fig. 2B). Secondly, the reaching error was significantly related with saccade RTs (Fig. 4A). Finally, reaching error in the horizontal direction was systematically biased by the direction of saccades (Fig. 4B). These results suggest that reaching movement incurs a cost when making saccades during reaching.

Several earlier publications have shown a direct co-dependence between eye and arm movements. For example, when producing concurrent eye and hand movements with different amplitude, reaching amplitude changed in accordance with saccade amplitude (54, 55). Similarly, the initial component of online reaching corrections to visual perturbation was modulated by whether saccade or gaze fixation was required (8). A recent study also showed that the relative eye-hand latencies of online corrections was modulated by the visual characteristics of the target change (56). These studies suggested the direct interaction of saccade planning/execution with reaching system, which can be flexible according to the task. Furthermore, some studies have emphasized a significant role of gaze-related signals for providing the representation of target location for reaching movements especially when making reaching in darkness. These studies showed that when participants made the spatially coupled or dissociated saccade during reaching, reaching accuracy was improved or worsened, respectively (57–60). This view of spatial coupling is also supported by the evidence that end points of saccade and reach are spatially correlated with each other (5, 61).

In contrast to these previous reports, showing that the hand follows the eye, we found that the hand deviated in the direction opposite to the saccade (Fig. 4B, Fig. 5). Such opposite bias can be explained by updating process of reaching goals dominated by eye-centered mechanisms (For review, see 62, 63). In our experimental setting, making a saccade changed the retinal position of the reaching target from fovea to peripheral. Such change can be made quickly and predictively via an internal updating process. Behavioral studies have shown that reaching to peripheral targets show systematic directional bias with overestimating the eccentricity of targets (64). When

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participants made a saccade before reaching, the resulting reaching error matched the updated target-gaze relationship (65, 66). More critically, this updating process can be seen during reaching movements: gaze shifts induced anti-directional deviations in the online reaching trajectory (67), as consistent with our current results.

As shown in Figure 5B, the hand responses generally preceded the initiation of saccades, suggesting that saccade planning, rather than saccade execution or saccade-related changes in visual inputs, drive the hand response. The hand response preceding saccade initiation is consistent with predictive updating of the target representation (68, 69). This temporal relationship was more prominent in the Hand condition where strong gaze-anchoring occurred. This also suggests that the inhibition of eye movements according to explicit reward demands arises after saccade planning has affected online reaching movements.

Reaching costs due to rapid saccades

We found that earlier saccades reduced reach accuracy more than late saccades (Fig. 4A). Previous studies on eye-hand coupling have mainly focused on visual acuity as cost for the reaching system: Locating objects in peripheral vision is less accurate than in foveal vision, which leads to lower reaching accuracy (e.g. 32, 70). Reaching accuracy highly depends on online information about the target and hand location (71–75). Thus, earlier saccades would withdraw this crucial information earlier, and spatial uncertainty would accumulate and be larger than when foveal feedback is withdrawn in the end of the movement.

Alternatively, the dependence of reaching accuracy on saccade RTs may be due to the fact that the saccade-induced hand deviation had more time to accumulate when the saccade is early. Although some studies have shown flexible use of a reference frame for motor actions and perception (76–81), we robustly observed the saccade-induced hand responses that were irrelevant to the current experimental task. This suggests that, in certain situations, planning/making saccades could be inherently linked with gaze-centered updating of the target (e.g. 82, 83). Such automatic updating process might be

20

584   one of the factors in causing saccade-related reaching cost.

585   While loss of visual acuity, as well as the influence of saccade planning on reach

586   trajectories, may have contributed to the relationship between saccade RT and reach

587   error (Fig. 4a), the presence of hand deviations that depend on saccade direction clearly

588   ague that at least part of the effect is due to influence of saccade planning on reaching.

589   It is worth to note that, similar to the error-RTs relationship shown in Figure 4A, the

590   difference of signed error at the endpoint between leftward- and rightward-saccade

591   conditions also appears to be greater ($p=0.08$, marginal significant effect) for trials with

592   earlier saccades (Appendix Fig. 2).

593

Summary

594

595   Taken together, our study tests two critical predictions of the hypothesis that

596   gaze anchoring is the result of an optimal feedback control policy that maximize reach

597   accuracy. First, we show that making an eye movement during an ongoing reach makes

598   the reach less accurate. Secondly, we demonstrate that probability of an early saccade

599   can be up- and down-regulated depending on the importance of reach accuracy. Of

600   course, our paper does not provide the most stringent test of optimal control theory in

601   this context, namely that the changes in feedback control are "optimal" in respect to a

602   well-defined cost-function. Nonetheless, our results confirm important, qualitative

603   predictions arising from the idea that eye-hand coordination is shaped to optimize task

604   performance.

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818   **Figure 1. Experimental setup and methods.** A: Experimental apparatus. B: Time course of a

819   single trial. Participants made reaching movements to a target (square of 1.5 x 1.5 cm) in a

820   forward direction. They had to make saccades in response to the shift in the fixation cross

821   while maintaining the reach to the target. C: Velocity trace (y-axis) for 3 example trials,

822   aligned to the detected start of the movement (0ms). Termination for each trace corresponds

823   to the detected end of movements. Vertical lines indicate the timing of fixation shift for

824   corresponding trial, occurring 2 cm into the movement. D: Sequence of experimental

825   sessions. Basic experimental task was the same across Base, Both, Eye, and Hand conditions.

826   In the Base condition, there was no reward. Reward was paid based on saccade performance

827   (Eye), reaching performance (Hand), and a combination (Both). Saccade only and Reaching

828   only conditions were conducted as a control. E: Payoff matrices for each reward condition.

829   See Materials and Methods for details.

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831
832   **Figure 2. Saccade reaction times and reaching error.** A: Mean saccade RTs across

833   participants (n=16) for three reward conditions. Error bars indicate standard error, and ***

834   denotes statistical significance with $p < 0.001$. B: Mean endpoint reaching error (distance from

835   the target), depending on whether a saccade was made and not made. Statistical significance

836   (***: $p < 0.001$) is shown for the comparison among three reward conditions.

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839   **Figure 3. Distribution of saccade RTs** A: Distribution of saccade RTs for each reward

840   condition obtained from two exemplary participants (P13 and P2, see Appendix Fig. A1 for

841   all participants). Magenta and cyan curves represent best fitting of data as obtained by

842   "Fixed-model" and "Flexible-model", respectively. Both models are based on bimodal log-

843   normal mixture distribution (Equation [2], See Method and Results for details). B: Fitting

844   curves split up by the first and second component. Each color corresponds to the reward

845   condition.

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847
848   **Figure 4. Relationship between reaching error and saccade.** A: Relationship between

849   reaching error (absolute value in the x-axis) and saccade RTs for three reward conditions.

850   The saccade trials were binned by saccade RTs for each participant and condition. Error bars

28

851   denote between-participants standard error (n=16). Reaching error for non-saccade trials was

852   also plotted. B: Mean reaching error (singed error in the x-axis) across participants for three

853   reward conditions with dividing the trials into saccade directions. Positive error values

854   reflect rightward biases. Error bars depict standard error.

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857   **Figure 5. Relationship between saccade and on-line hand response.** A: Mean x-hand

858   velocities against the time from the fixation cross displacement. The hand responses were

859   induced in the opposite direction from the saccade. Shaded area: SD across participants

860   (n=16). B: We took the difference in the hand velocity between trials with leftward and

861   rightward saccades (leftward-rightward). Shown is the mean response across participants

862   for each reward condition. Arrows indicate the averaged saccade RTs for each condition.

863
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865   **Appendix Figure A1**

866   Distribution of saccade RTs (Top: Eye, Middle: Both, and Bottom: Hand condition) for each

867   participant (P1 – P16). Magenta and cyan curve illustrates the fit of "Fixed-model" and

868   "Flexible-model", respectively.

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870

871   **Appendix Figure 2. Relationship between signed reach error and saccade RTs.**

872   The signed reach error in the x-axis at the endpoint was averaged across each direction of

873   the saccade. The difference in the mean error between leftward- and rightward-saccade

874   conditions was plotted against the saccade RTs (three bins). Data represent the mean and

875   standard error across participants. Two-way repeated measures ANOVA with Reward (Eye,

876   Both, or Hand) and Bin (three RTs bins) as main factors showed a non-significant main effect

877   of Reward ($F_{(2,30)}=0.69$, $p=0.51$) and a marginal significant main effect of Bin ($F_{(2,30)}=2.69$,

878    $p = 0.08$). The interaction effect was not significant ($F_{(4,60)}=1.208$ $p=0.38$).
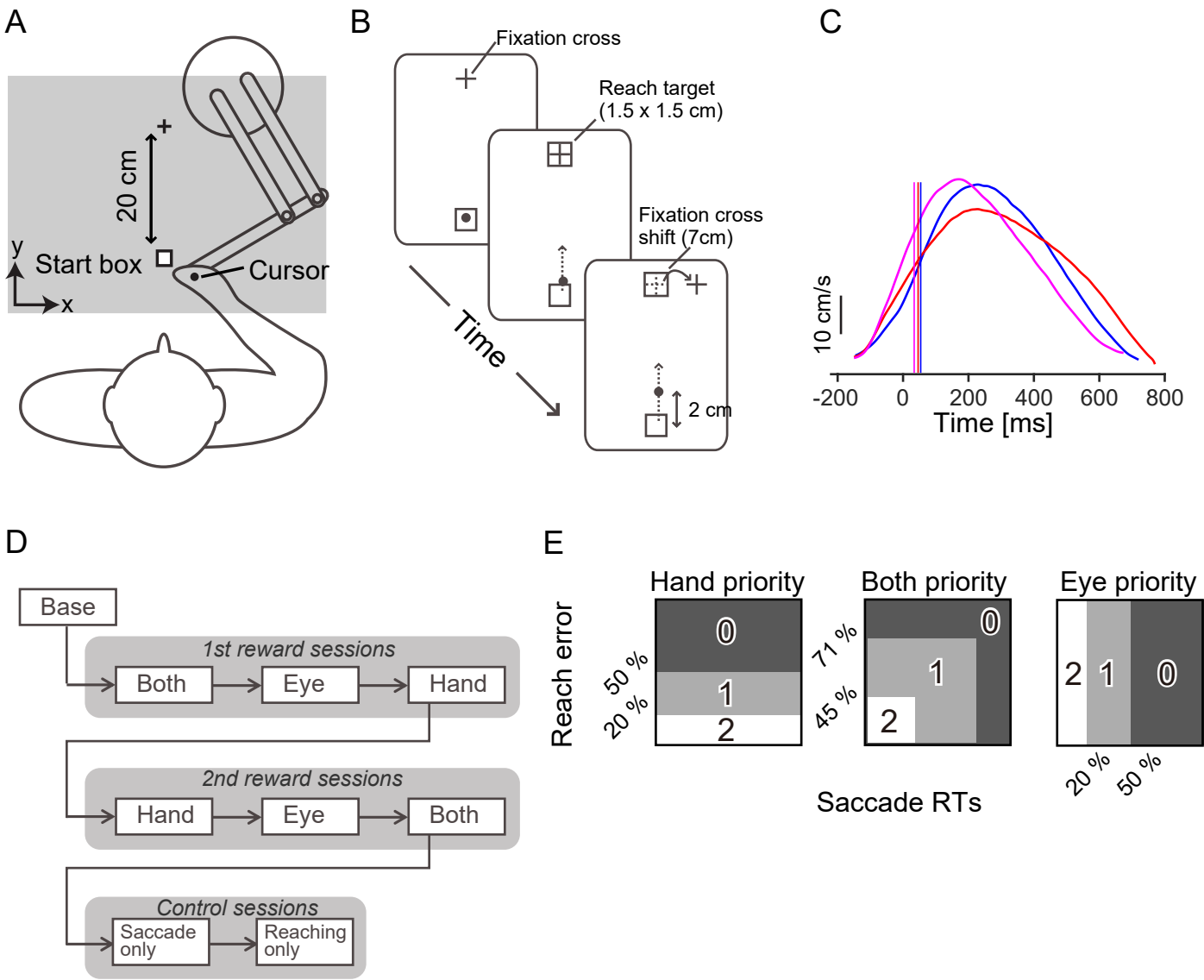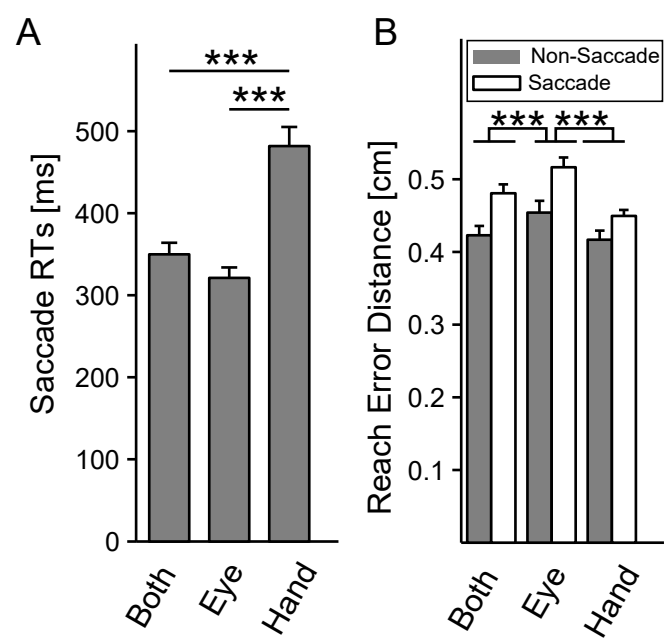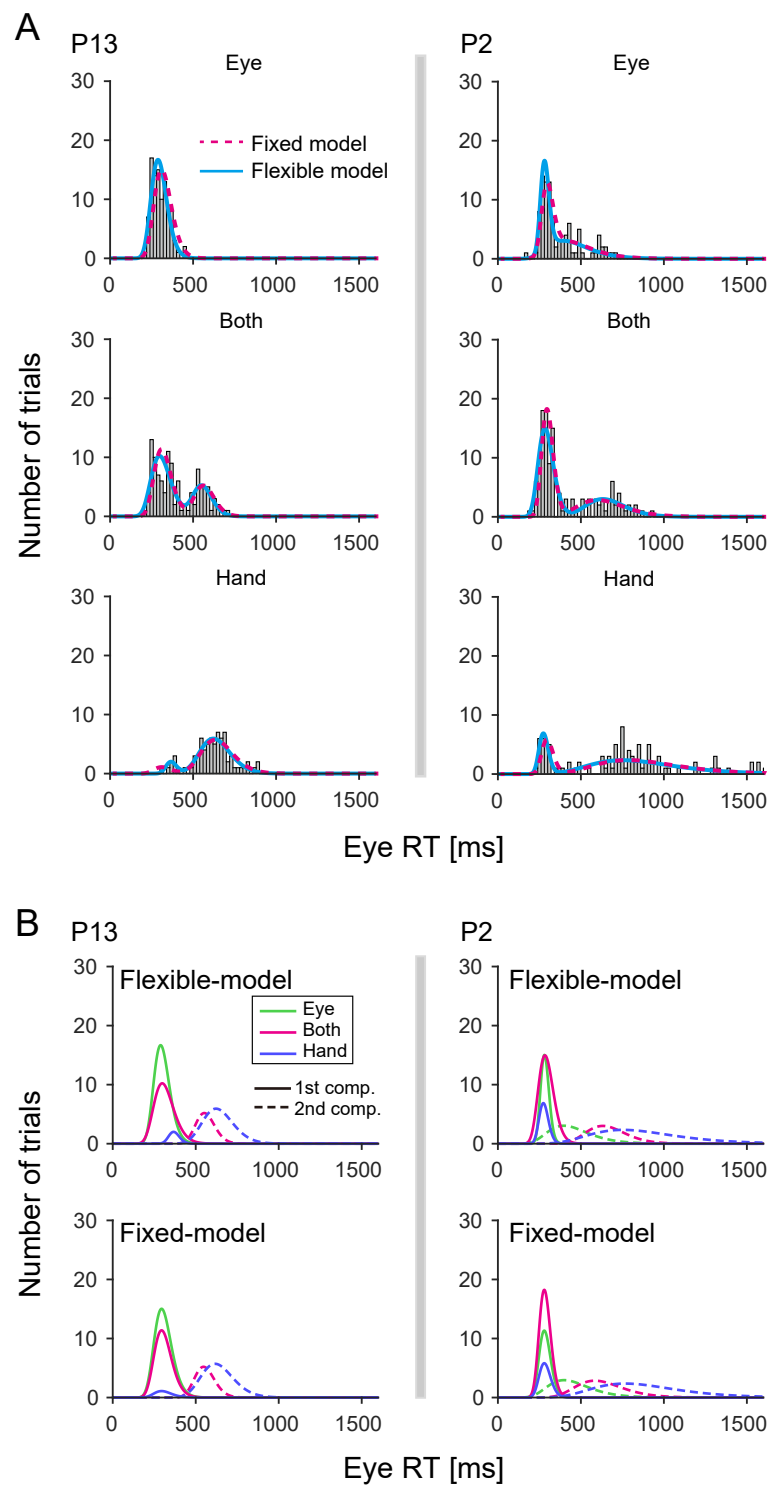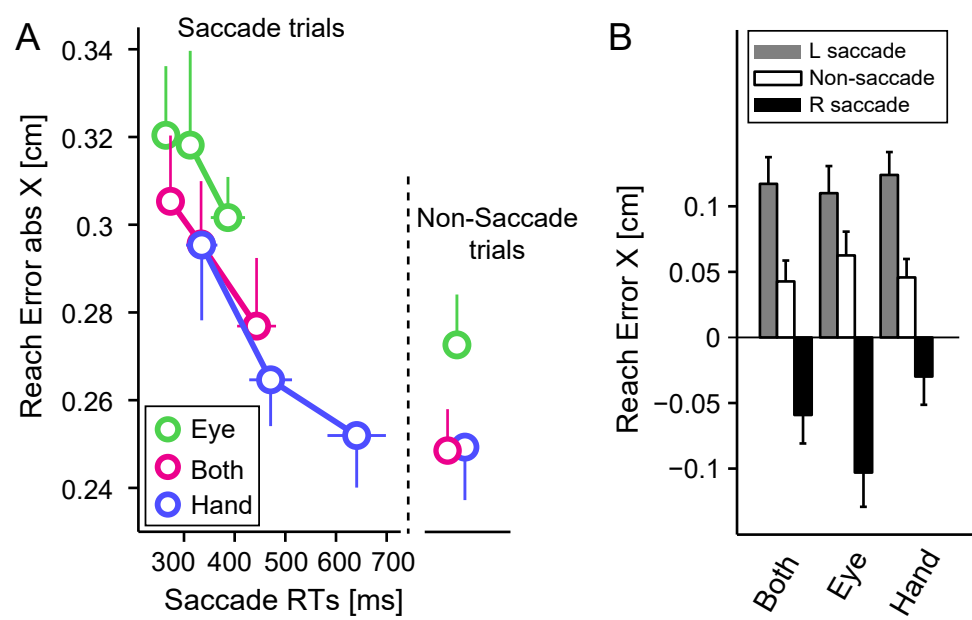
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Figure 1
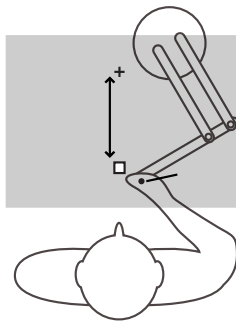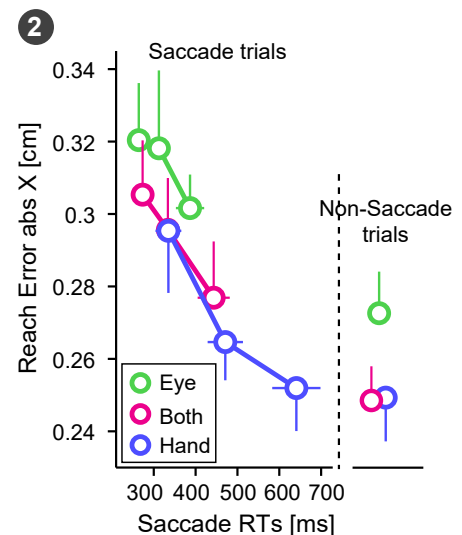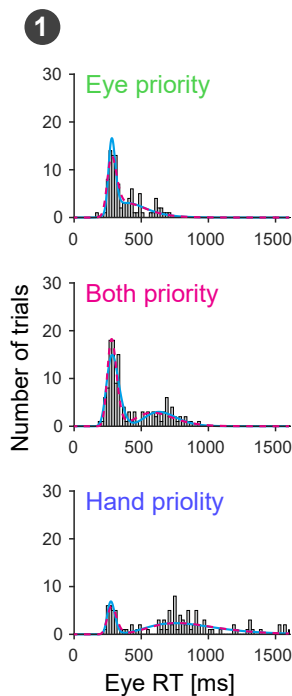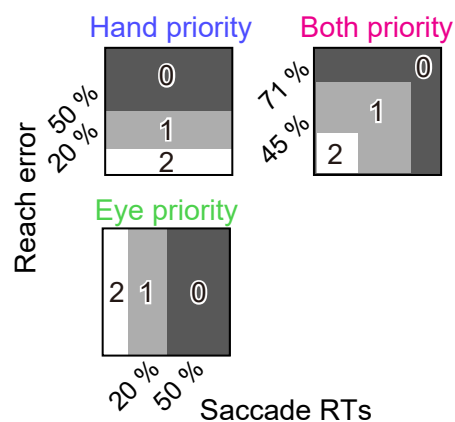
Figure 2

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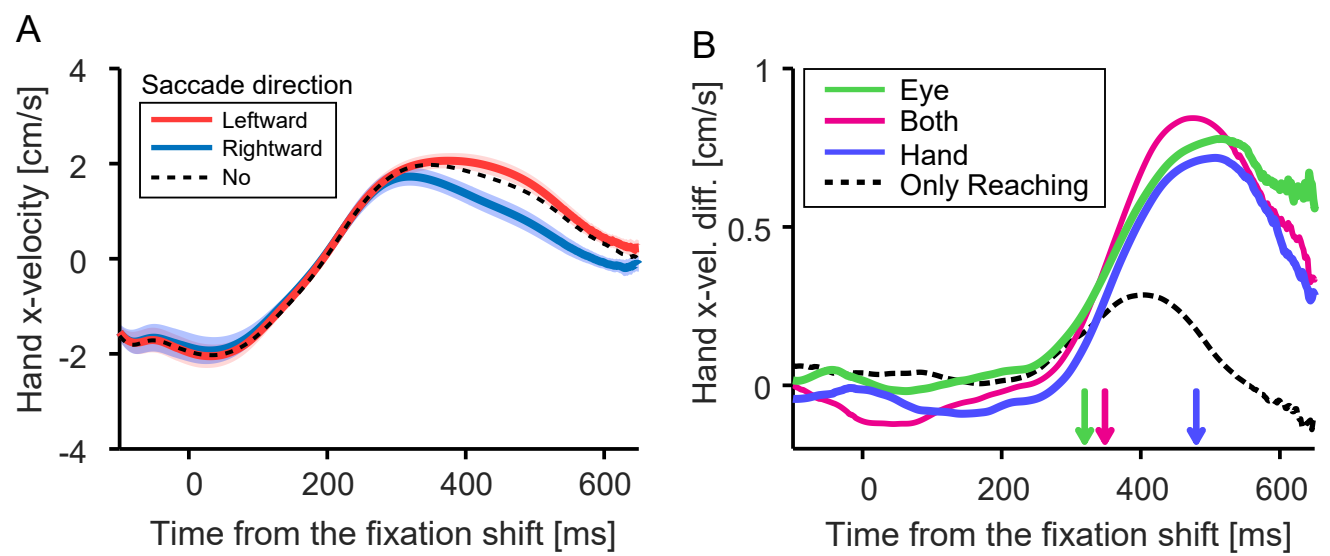
During reaching, saccades away from the target are delayed (gaze-anchoring).

Payoff matrices for each reward condition

Hand priority Both priority

Eye priority

Reach error

Saccade RTs

1 **2** Saccade RTs and reach error varied systematically with the reward contingencies, with reach accuracy improving with later saccades.

1 The chnage in saccade RTs is mainly achieved by the modulation of the probability of fast saccades.

Gaze-anchoring acts through a suppression of fast saccades, a mechanism that can be adaptively adjusted to the current task demands.

Appendix Figure 1

Eye RT [ms]

Eye RT [ms]

Appendix_Figure2