Previous motor actions outweigh sensory information in sensorimotor learning

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Abstract

Humans can use their previous experience in form of statistical priors to improve decisions. It is however unclear how such priors are learned and represented. Importantly, it has remained elusive whether prior learning is independent of the sensorimotor system involved in the learning process or not, as both modality-specific and modality-general learning have been reported in the past. Here, we used a saccadic eye movement task to probe the learning and representation of a spatial prior across a few trials. In this task, learning occurs in an unsupervised manner and through encountering trial-by-trial visual hints drawn from a distribution centered on the target location. Using a model-comparison approach, we found that participants' prior knowledge is largely represented in the form of their previous motor actions, with minimal influence from the previously seen visual hints. By using two different motor contexts for response (looking either at the estimated target location, or exactly opposite to it), we could further compare whether prior experience obtained in one motor context can be transferred to the other. Although learning curves were highly similar, and participants seemed to use the same strategy for both response types, they could not transfer their knowledge between contexts, as performance and confidence ratings dropped to naïve levels after a switch of the required response. Together, our results suggest that humans preferably use the internal representations of their previous motor actions, rather than past incoming sensory information, to form statistical sensorimotor priors on the timescale of a few trials.

Introduction

We often have to make decisions based on sparse and uncertain sensory information. Previous research has shown that in these cases humans use Bayesian inference where the current sensory information (likelihood) and the previously acquired knowledge (priors) are integrated, each weighted by their respective uncertainty [1,2]. While the majority of previous studies have examined whether the perceptual and sensorimotor decisions follow the rules of a Bayesian framework [1,3], less emphasis has been placed on understanding how likelihoods and especially statistical priors are learned and represented in the first place. A number of elegant recent studies have tried to bridge this gap by investigating how people learn likelihoods [4] and priors [5] to perform Bayesian computations. Interestingly, the timescale of the two types of learning varied vastly, with fast learning of likelihood but slow learning of prior distributions. It remains unknown why such an asymmetry should exist, as theoretically both types of learning are equivalent. It has been hypothesized that learning about the likelihood versus learning about the prior involves different neural mechanisms, potentially hinting to the fact that their respective distributions might be represented in different regions of the brain [6] .

Learning of statistical priors is itself not a uniform process as it shows dependencies on the specific context where the learning occurs. In Bayesian framework, priors are a form of abstract knowledge [7–9], which can be generalized across different contexts. However, previous findings regarding the generalization of statistical priors have been mixed. Some studies have shown that statistical learning of priors is very narrow-band and context/modality-specific in perceptual [10] and sensorimotor domains [11,12], thus preventing learned information to transfer to different contexts/modalities. Other studies, on the other hand, provided evidence for generalization [4,13], although generalization, in some instances, seemed to occur differently for different parameters of a statistical distribution; e.g. the mean and the variance of a distribution [14]. The finding that some aspects of learning could generalize, while others could not, was confirmed by a recent study showing that, for instance, in Bayesian time estimation, priors can be generalized across stimuli, but not motor actions [15].

Therefore, despite an increasing number of studies testing generalization and transfer, the exact rules determining generalizability remain unclear. One potential reason for these seemingly contradictory results is a lack of a formal definition of *what* is learned. It has been argued that when learning is not generalized, a *policy* (i.e. a specific rule for action) rather than *knowledge* (i.e.

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91   abstract and context-independent information) is acquired through learning [16]. However, it is
92   not clear what features of the learning dynamics determine whether a *policy* or *knowledge* is
93   acquired during encounters with the learned information.

94   To investigate learning and generalizability of a prior distribution, we employed a saccadic eye
95   movement task similar to the design of a previous study [17], where participants had to learn to
96   locate a hidden target. The location of the hidden target corresponded to the mean of a circular
97   normal distribution. In each trial, a visual hint sampled from the underlying distribution was shown
98   and participants indicated their current estimate with a saccadic eye movement, looking either
99   towards (pro-saccade) or to the exact opposite direction of the target (anti-saccade). To
100   successfully estimate the hidden target location, participants had to combine information across
101   multiple trials. This design allowed us to investigate whether participants formed their prior
102   knowledge by combining the visual information or by combining the previous motor actions across
103   time, under different saccadic response contexts. Our results from two experiments indicate that
104   sensorimotor learning of a spatial prior in both response contexts is largely guided by previous
105   motor plans, rather than by previous sensory input in form of visual hints. Despite the high degree
106   of similarity of pro- and anti-saccades in their learning behavior, suggesting a motor-independent
107   learning algorithm, the learned prior in one context did not generalize to the other. We propose
108   that the lack of transfer between the two contexts is a natural consequence of their shared learning
109   algorithm in which previous motor actions outweigh sensory information.

Results

111   To investigate the dynamics of sensorimotor learning of a spatial prior and its dependence on the
112   response modality, we designed an experiment where participants had to find a hidden target and
113   indicate their guess by either a pro- or an anti-saccade. Participants learned the location of each
114   hidden target within twenty trials, of which a block of ten trials required pro-saccades and the other
115   block of ten trials required anti-saccades as the response modality (**Fig.1 A**). This design allowed
116   us to probe whether the learning dynamics shows dependencies on the response modality, hence
117   being modality-specific. We also used another task, referred to as the calibration task, to estimate
118   each participant's motoric noise during the visually driven execution of pro- or anti-saccades. In
119   contrast to the calibration task, in the hidden target task the main error source is the uncertainty
120   regarding the hidden target location. As the same motor system is used in both the hidden target

121   task as well as the calibration task, we assumed that the motor noise affecting participants'

122   performance in both tasks is equal. As the motor noise in the calibration task is not time-dependent,

123   we assumed that all time-dependent performance improvement during the hidden target task

124   reflected statistical learning, defined as the reduction in the uncertainty regarding the location of
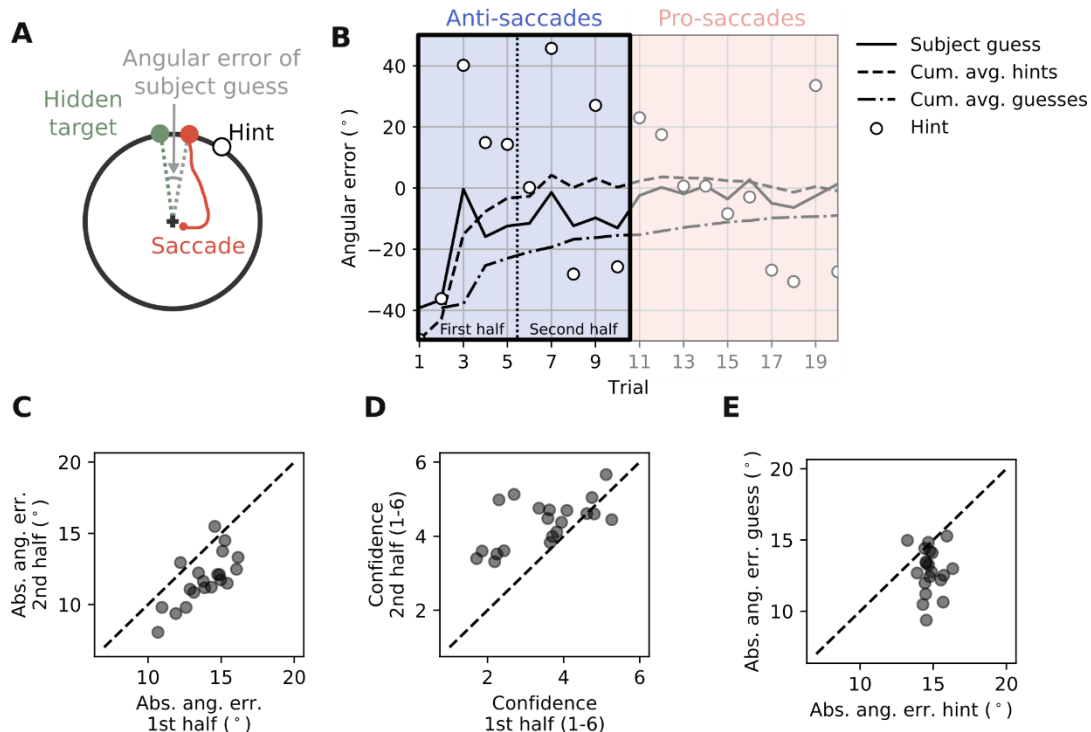
125   the hidden target.
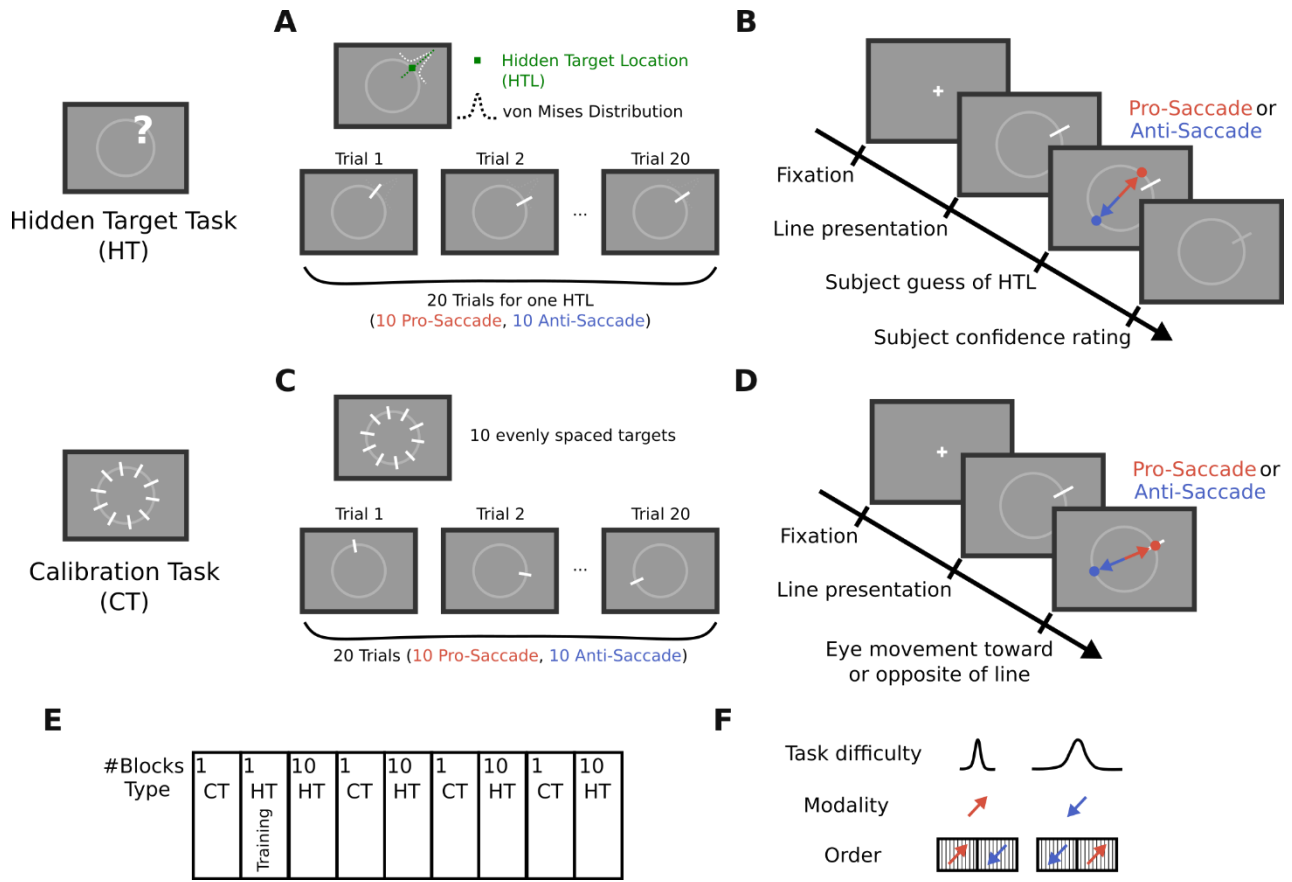
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127   **Figure 1:** *Experimental design of the hidden target task employed to study the statistical learning of a spatial prior*
128   *in two different visuo-motor contexts.* (A-B) Main task of the experiment. (A) Participants were told to estimate the
129   location of a 'hidden treasure' on a ring by observing and combining information provided by the visual hints across
130   trials. The hidden target location was defined as the mean of a von Mises distribution and the hints, presented at each
131   trial, were samples drawn from this underlying distribution. Participants had twenty trials to estimate the location of
132   the hidden target, after which a new hidden target had to be found. Participants used their gaze to indicate their
133   responses. (B) Each trial started with a fixation period, after which the hint was presented, and participants had to
134   indicate their guess about the location of the hidden target by either looking at it (pro-saccade response) or by looking
135   exactly opposite to it (anti-saccade response). In half of the trials (i.e. consecutive 10 trials), participants had to use
136   pro-saccades, and in the other half they used anti-saccades, with a randomized order across blocks. (C-D) Calibration
137   task used to estimate the motoric error of each participant for pro- and anti-saccades. Participants had to directly look
138   either at the lines (pro-saccade response) or exactly opposite to the lines (anti-saccade response). (E) Block-design of
139   the experiment. (F) We compared learning across two levels of difficulty and two different response types. Task
140   difficulty was varied by changing the standard deviation of the von Mises distribution. Finally, we tested whether
141   knowledge could be transferred from one visuo-motor context to the other. For this we also varied the order of pro-
142   saccade and anti-saccade responses across blocks.

143

144 Participants successfully accumulate information and learn on a short time scale

145 To establish that participants were in general able to learn on a short timescale, we initially focused

146 on the first ten trials of each hidden target block (**Fig.2 B**). In this case, in all ten trials participants

147 responded by using the same modality, either exclusively by pro-saccades, or exclusively by anti-

148 saccades. To quantify performance, we calculated the absolute angular error between the saccade

149 endpoint and the hidden target location (**Fig.2 A**). By comparing the average absolute angular error

150 in the first five trials with the average absolute angular error in the last five trials, we found that

151 most of the participants were able to improve their estimates of the target location (i.e. their

152 guesses) during this short timescale (paired t-test: t=7.25, p<0.0001, N=20) (**Fig.2 C**). In line with

153 performance, participants' confidence about the accuracy of their guesses increased during the ten

154 trials (paired t-test: t=-4.39, p=0.0003, N=20) (**Fig.2 D**). Additionally, the absolute angular error

155 of participants' guesses was lower than the absolute angular error of the visual hints, meaning that

156 participants' guesses were closer to the center of the von Mises distribution compared to the

157 presented visual hints (paired t-test: t=4.92, p=0.0001, N=20) (**Fig.2 E**). This shows that

158 participants were able to combine information across trials and thereby improve their estimates of

159 the target location, rather than just following the current visual hint. Hence, we can conclude that

160 participants showed some form of statistical learning during the first ten trials of the hidden target

161 task.

162

163 **Figure 2:** *Participants successfully learn the most probable location of the target on a short time scale.* (A) The
164 angular difference between the participants' guess and the true location of the hidden target was used to measure
165 learning. (B) Example block. To test learning, we compared the performance in trial 1-5 (first half) to the performance
166 in trial 6-10 (second half). (C) The absolute angular error in the second half is lower than in the first half (paired t-
167 test: t=7.25, p<0.0001, N=20). (D) Participants' confidence is higher in the second half than in the first half (paired t-
168 test: t=-4.39, p=0.0003, N=20). (E) The absolute angular error of participants is lower than the absolute angular error
169 of the visual hints, i.e., participants' guesses are closer to the center of the von Mises distribution compared to the
170 presented visual hints (paired t-test: t=4.92, p=0.0001, N=20).

171 **Learning curves are stereotypic across response modalities**

172 To work out whether statistical learning is modality-dependent or not, we contrasted the learning

173 performance in pro- versus anti-saccade trials in the hidden target task, as well as in the calibration

174 task. First, we quantified the mean and the standard deviation of the respective angular error

175 distributions, pooled across participants (**Fig.3 A&B and Table 1**). We did not find a significant

176 bias towards a specific direction, either clockwise or counter-clockwise (one-sample t-test; mean

177 different from zero; N=20; **Table 1**), for any of the distributions.

178

Task	Modality	Mean	SD	p-value
Calibration	Pro-saccade	-0.1°	6.3°	0.48
Calibration	Anti-saccade	0.7°	9.5°	0.15
Hidden target	Pro-saccade	1.1°	16.9°	0.11
Hidden target	Anti-saccade	0.1°	18.4°	0.99
Hidden target	Hints	0.1°	20.6°	0.60

179 **Table 1:** *Angular error distribution for calibration and the hidden target task.* Mean and standard deviation for
180 distributions shown in Fig. 3A&B. We tested whether the mean of either of the five distributions was significantly
181 different from zero (one-sample t-test; N=20). The corresponding p-values are shown in the last column.

182 For both modalities, the standard deviation of the angular error was higher in the hidden target task

183 than in the calibration task (pro-saccades: paired t-test, t=-11.8, p<0.0001, N=20 / anti-saccades:

184 paired t-test, t=-10.9, p<0.0001, N=20), which is plausible as in the former task participants were

185 more uncertain of the target location. Furthermore, the standard deviations of pro- and anti-

186 saccades were only significantly different during the calibration task but not during the hidden

187 target task (calibration: paired t-test, t=-3.8, p=0.0011, N=20 / hidden target task: paired t-test, t=-

188 1.7, p=0.1108, N=20). To quantify this difference further, we calculated a modality difference

189 index (described in Materials and Methods section), which was significantly higher in the

190   calibration task compared to the hidden target task (paired t-test, t=-6.44, p<0.0001, N=20,

191   **Fig.3 C**). These results provide the first evidence that statistical learning is modality-independent.

192   To see whether there is a difference between pro- and anti-saccades depending on the difficulty of

193   the task, we next looked at the influence of both experimental factors (pro-/ anti-saccade response,

194   broad/narrow hint distribution) on participants' performance. To this end, we conducted a linear

195   mixed model analysis of the single trial data (i.e., the absolute angular error), with *task difficulty*

196   and *response type* as fixed effects and participant identity as random effect. Using this statistically

197   more powerful approach, we found a main effect of task difficulty (t=20.6, p<0.0001; contrast:

198   easy-hard=-8.28°±0.27°(SE), t=-31.2, p<0.0001), as well as response type (t=2.0, p=0.0469;

199   contrast: pro-anti=-1.32°±0.27°(SE), t=-5.0, p<0.0001). Additionally, an interaction effect was

200   found between the task difficulty and response type (t=2.2, p=0.0299), indicating that there is only

201   a difference between pro- and anti-saccade responses in the hard task condition (hard_pro-

202   hard_anti=-1.90°±0.38°(SE), t=-5.035, p<0.0001; easy_pro-easy_anti=-0.74°±0.37°(SE), t=-

203   1.988, p=0.1927). The same pattern was found when we examined participants' confidence

204   ratings: participants were more confident in pro-saccade trials and in the easier task condition

205   (main effect *response*: t=-4.2, p<0.0001, contrast: pro-anti=0.28±0.03, t=10.3, p<0.0001 / main

206   effect *difficulty*: t=-9.25, p<0.0001, contrast: easy-hard=0.47±0.03, t=17.4, p<0.0001 / interaction

207   effect: t=-4.4, p<0.0001). These results show that there is a small influence of the used visuo-motor

208   modality on participants' performance and confidence in the hidden target task, if the hint

209   distribution is broad (hard task condition). As shown in **Fig.3 A-C**, this difference is much smaller

210   than the difference we observed in the calibration task.

211   To investigate whether the response type had an influence on the statistical learning itself, we

212   included the trial number as another fixed effect in our linear mixed model (as a continuous

213   variable). If the response type influenced participants' performance in a trial-independent manner,

214   it would act as a general offset. In contrast, if statistical learning were modality-dependent, we

215   would expect an interaction between the trial number and the response type (pro- versus anti-

216   saccades). Visual inspection of the learning curves for pro- and anti-saccade responses suggested

217   the former, and the main effect influencing the shape of the learning curves seemed to be the task

218   difficulty (**Fig.3 D-E**). For participants' performance, measured as the absolute angular error, we

219   found a significant main effect of difficulty (t=21.4, p<0.0001) and a significant interaction

220   between trial number and difficulty (t=-7.807, p<0.0001), but no significant interaction between

221 trial number and response type (t=0.650, p=0.516). Further analysis of the interaction effect
222 showed that only for blocks with high task difficulty there is a significant effect of trial number
223 (hard: slope=-0.84±0.08, t=-10.57, p<0.0001 / easy: slope=-0.12±0.08, t=-1.50, p=0.13). This
224 result was further supported by the analysis of the confidence ratings, as participants' confidence
225 time course (**Fig. S1**) was also mainly dominated by the influence of task difficulty (interaction
226 effect *trial* x *difficulty*: t=-8.858, p<0.0001) and not by the response type (interaction effect *trial* x
227 *response*: t=-1.006, p=0.315). Together, these results show that both performance and confidence
228 increase in a modality-independent manner during learning of a spatial prior.
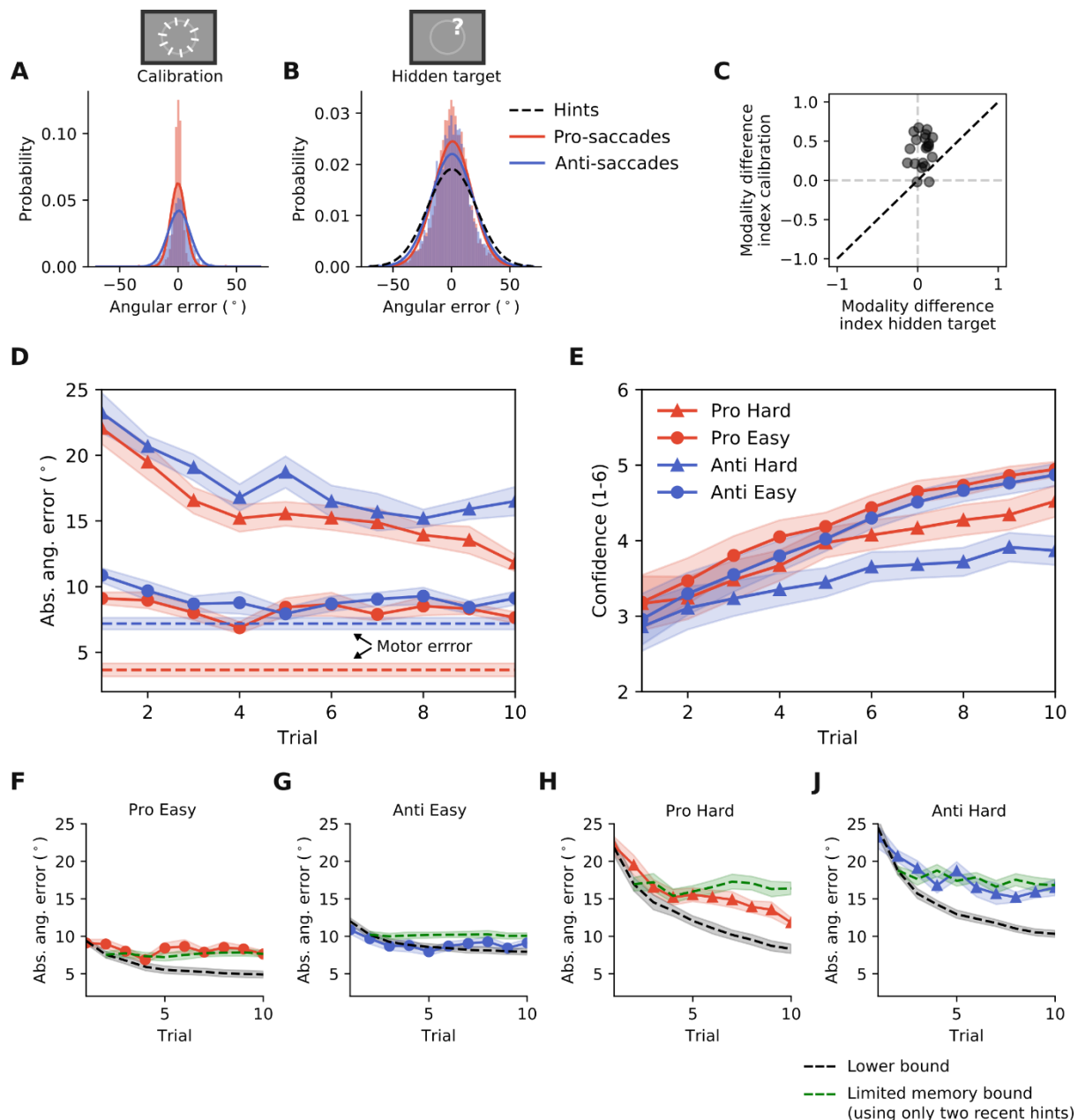
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230 **Figure 3:** *Learning curves are stereotypic across response modalities.* (A) The distribution of the angular error for
231 pro- and anti-saccade response in the calibration task. (B) The distribution of the angular error for pro- and anti-
232 saccade response in the hidden target task. (C) Comparison of pro-/anti-saccade performance difference between the
233 hidden target task and the calibration task. (D) Time course of the absolute angular error for each of the four different
234 conditions (two response types x two difficulties). Here and in the following panels, except stated otherwise, shaded
235 areas represent the standard error of the mean (N=20) (E) Time course of the confidence ratings for each of the four
236 different conditions. (F-J) Participants' learning curves compared to the lower bound and the limited memory bound.
237 The lower bound is given by taking the cumulative average of all hints presented so far and adding the error due to
238 the noise in the motor plans, estimated from the calibration task. The limited memory is similarly calculated, except
239 that only the latest two hints are used.

Performance is suboptimal

241 Since at each point in time, participants have only seen a limited number of samples from the

242 underlying distribution of the target location (in form of visual hints), it is theoretically impossible

243 to correctly estimate the distribution's mean, i.e., the hidden target location in our task. In principle,

244 only for an indefinite number of samples, the sample mean equals the population mean. For the

245 hidden target task, this means that participants could theoretically only reach zero absolute angular

246 error if an infinite number of trials were seen. Taking this into account, we can compare

247 participants' performance to the time course of the theoretical statistical uncertainty due to seeing

248 a limited number of samples (i.e., sampling error, see also Materials and Methods section). This

249 provides a lower bound on participants' uncertainty, indicated by the variance of angular errors

250 σ^2:

251   1) $\sigma^2 = \sigma_{motor}^2 + \sigma_{sample}^2 = \sigma_{motor}^2 + \frac{\sigma_{dist}^2}{n}$

252 where n is the number of visual hints seen so far, σ_{dist}^2 is the variance of the von Mises distribution

253 and σ_{motor}^2 is the motoric noise measured in the calibration task. We can then calculate the

254 theoretical optimal performance in terms of the mean absolute angular error from this optimal

255 variance estimate (see Eq 2 in Materials and Methods section). Comparing participants'

256 performance to this lower bound shows that for the first trial in each hidden target block,

257 participants perform as well as they possibly can (**Fig.3 F-J**), independent of the task difficulty or

258 the used response modality – pro- or anti-saccades. However, as soon as they need to combine

259 multiple samples to estimate the hidden target location, they perform suboptimal (**Fig.3 F-J**, black

260 dashed line is optimal). We hypothesized that the reason for this suboptimal behavior is limited

261 memory, as to perform optimally would mean to remember every single hint which has been

262 presented so far. So instead of calculating the cumulative mean of all visual hints presented so far

263 (which results in optimal performance), we calculated the performance estimate for an alternative

264   strategy where subjects only average the latest two visual hints (**Fig.3 F-J** green dashed line). This

265   limited memory estimate could describe participants' performance qualitatively better, as it

266   captured the shallower learning curves for both response types. In summary, the analysis of

267   different aspects of performance did not show large differences in statistical learning between pro-

268   and anti-saccades.

269   **Strategy is modality-independent**

270   So far, we have seen that statistical learning in the pro- and in the anti-saccade context is similar

271   in terms of the absolute performance and the shape of the learning curve. Next, we wanted to test

272   whether participants use different strategies in the pro- versus in the anti-saccade blocks. The first

273   candidate strategy would be to only look at the visual hints in each trial, which would mean that

274   no learning is happening, and that participants' behavior is only visually-driven. Instead, the

275   optimal strategy, which would result in the lower bound we calculated before, would be to

276   calculate the cumulative average of every hint seen so far in each trial. Besides taking into account

277   the hints, visually presented to the participants, we can also imagine that the behavior is driven by

278   an internal state that promotes looking close to where one has been looking before, i.e., to follow

279   previous guesses (**Fig.4 A**). To test these different hypotheses, we fitted several single predictor

280   linear regression models, for each proposed strategy. Through a model comparison (see Materials

281   and Methods for the details) we found that the best single predictor model is the cumulative

282   average of previous guesses (**Fig.4 B**). Splitting the data into pro- and anti-saccade blocks and

283   repeating the analysis showed that the best single predictor model does not depend on the used

284   response type (**Fig.4 C-D**). Thus, this provides another piece of evidence that the statistical

285   learning happening in our task is independent of the response type.

286   In a second step, we also tested several multi-predictor models to get a more detailed view on

287   participants' strategy. We tested multiple combinations of past guesses, and past and present visual

288   hints. Models based on the previous three guesses or the current and previous three visual hints

289   did not perform as well as the best single predictor model. In contrast, models which relied on

290   combinations of external and internal information, i.e., the visual hints and previous guesses,

291   performed as well as the best single predictor model, even if they only looked three time steps in

292   the past (**Fig.4 B**). Again, splitting the data into pro- and anti-saccade blocks did not affect the

293   main trend (**Fig.4 C-D**).

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294   Lastly, to find the exact weighting participants put on their previous guesses and the current and

295   previous hints, depending on the used response type, we fitted a model with all three previous

296   guesses, the current and three previous hints, and the response type as predictors. We found that

297   participants used external information only from the current trial, ignoring the hints from previous

298   trials (**Fig.4 F**). Instead, to combine information across trials they relied on their internal

299   estimations from the past (**Fig.4 E**). We obtained similar results when models that only included

300   either the past guesses or the past visual hints were tested **(Fig. S5)**. Including the response type in

301   the model allowed to estimate separate regression weights for pro- and anti-saccades. Again, we

302   didn't find any significant difference in the weighting participants put on their own guesses versus

303   given hints, depending on whether they use pro- or anti-saccades for response (**Fig.4 E-H**; paired

304   t-test: n.s.). In summary, we found that participants used the same strategy, regardless of the

305   response type, to solve the task, which provides further evidence for the modality-independent

306   learning hypothesis.
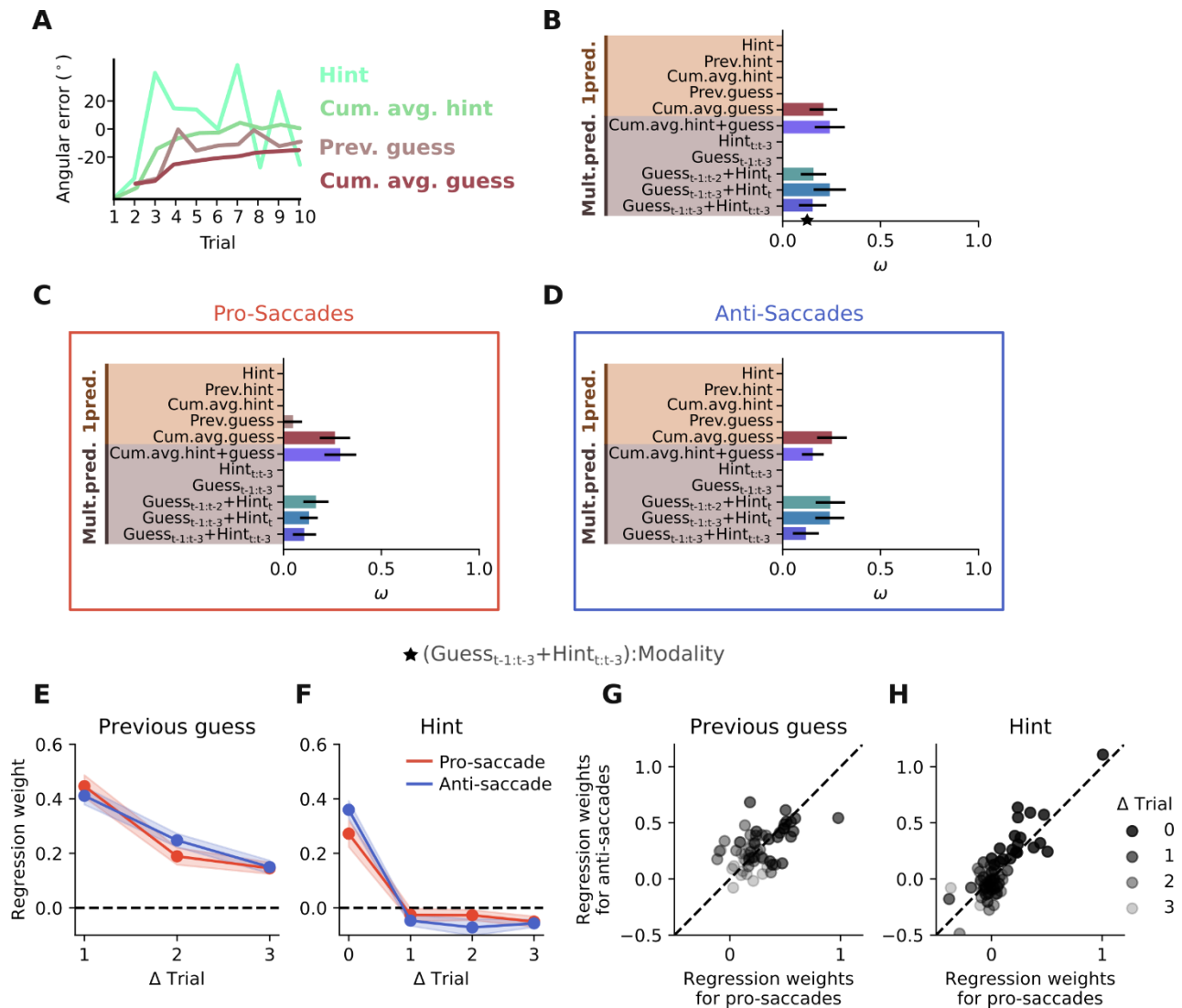
Figure 4: *Strategy is modality-independent.* (A) Different predictors used to explain the participants' single trial estimates. (B) Model comparison between various single and multiple predictor models. Shown are the weights ω, which represent the probability that a model is the best among the ones considered. (C-D) Same as (B) but performed on two different data sets, one consisting only of pro-saccade response trials, the other consisting only of anti-saccade response trials. (E-H) Regression weights for a model including participants' last three guesses and the current and last three visual hints. (E) Regression weights put on the last three guesses. (F) Regression weights put on the current, as well as the last three hints. (G-H) Participants put similar weight on guesses and hints in pro- and anti-saccade response trials (paired t-test; n.s.).

Drop in performance after response switch

Despite the similarity in performance and observed strategy, hinting at a general algorithm used for statistical learning in our task, it is still possible that learning happens for each visuo-motor

320   modality in a very specific manner and that both just look similar in terms of performance and

321   strategy. In this case, it would not be possible to generalize between modalities. To test this, we

322   included trial eleven until twenty where participants had to continue looking for the same hidden

323   target (and were also instructed that all twenty trials belong to one hidden target), but had to use

324   the other visuo-motor modality than in trial 1 until 10 (**Fig.5 A**). We considered two alternative

325   hypotheses. The first states that participants learn in a modality-independent fashion and store the

326   acquired knowledge in an abstract form, which allows a complete transfer of previous experience

327   to a new response modality after a switch (**Fig.5 B**, black solid line). The second hypothesis would

328   be that participants perform trial eleven until twenty as if there was no previous experience, which

329   would suggest a modality-specific implementation of the learned knowledge (**Fig.5 B**, gray dashed

330   line). To test which of these hypotheses is true, we compared the performance in trial 10 (last trial

331   before response switch) to the performance in trial 11 (first trial after response switch). We found

332   that the performance is significantly worse in trial 11 than trial 10 (paired t-test, t=-6.5, p<0.0001,

333   **Fig.5 C**). The performance decrease in trial 11 was consistent across all 4 conditions (**Fig.5 F**).

334   This shows that there is no direct transfer of knowledge across response types. After ruling out the

335   modality-general implementation, we wanted to test if there is any measurable interaction between

336   the first ten trials and the second ten trials. For this, we compared the starting points of each

337   learning curve – trial 1 and trial 11 (**Fig.5 D**), as well as the end points of each learning curve –

338   trial 10 and trial 20 (**Fig.5 E**). There was no significant difference between these, suggesting that

339   the learning curves are identical. These results were corroborated by analyzing confidence ratings,

340   as we also observed a drop in confidence at trial 11 compared to trial 10, in line with our results

341   on performance (paired t-test trial 10 - trial 11, t=3.7, p=0.0016, **Fig. S1&S2**)
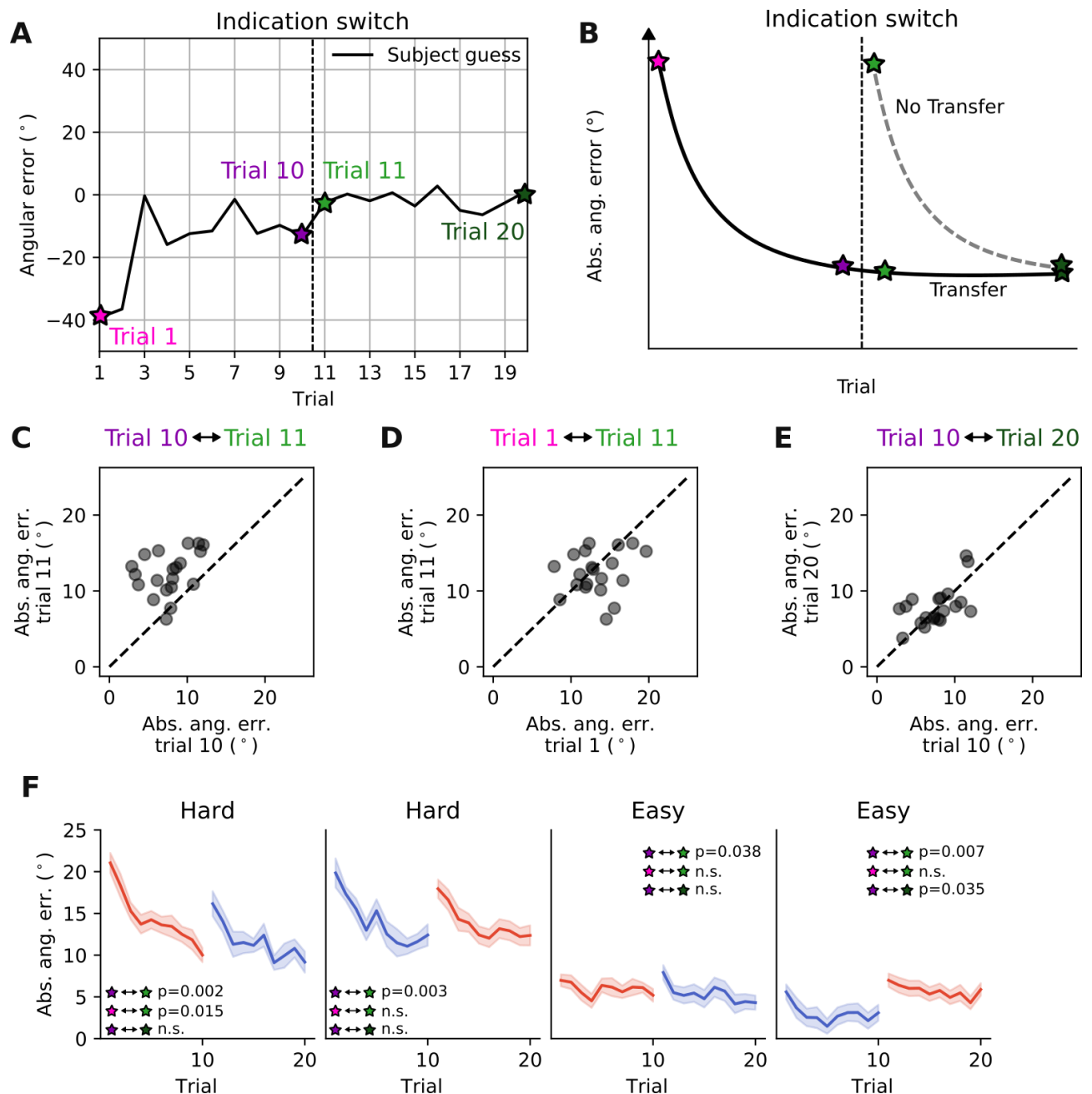
Figure 5: *Drop in performance after response switch.* (A) To test the knowledge transfer hypothesis, we analyzed all trials within a block, encompassing trials before and after the switch. We specifically focused on the difference between trial 10 (before response switch) and trial 11 (after response switch). (B) If knowledge is transferred, we expect similar performance in trial 11 as in trial 10. In contrast, if no knowledge is transferred, we expect trial 11 to show similar performance to trial 1. (C) Performance in trial 11 is worse than in trial 10 (paired t-test, t=-6.5, p<0.0001). (D) Performance in trial 11 is similar to performance in trial 1 (paired t-test; n.s.; N=20). (E) Performance in trial 10 is similar to performance in trial 20 (paired t-test; n.s.; N=20). (F) Performance time course for different difficulty levels and pro-/anti-saccade orders. To illustrate the difference due to statistical learning only, we subtracted the motor error estimated from the calibration task. Insets show the result for the same statistical test as in (C-E), but performed separately on the data of each condition.

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355 **No knowledge transfer between visuo-motor modalities**

356 As modeling showed that participants rely on their previous guesses rather than previously seen

357 visual hints (**Fig.4 E**), we wished to test whether this is also the case across the time that a response

358 switch occurs. For this, we calculated the regression weights on previous guesses in a time-

359 dependent manner (**Fig.6 A**). If knowledge is not transferred between different visuo-motor

360 modalities we would predict: 1) Participants highly rely on the visual hint in trial 11 and do not

361 use previous guesses to inform their decision. 2) They are also not able to use previous guesses

362 further in the past, if these guesses were obtained before the response switch. Our analysis showed

363 that indeed these were the case. We found that participants' estimates in trial 11 (after response

364 switch) are independent of their guess in trial 10 (before response switch). In contrast, at all other

365 time points they used previous guesses to inform their current decision (**Fig.6 B**). As participants

366 did not use their previous experience in trial 11, we expected that they instead rely highly on the

367 hint presented in trial 11. Regression analysis confirmed this hypothesis (**Fig.6 C**), although we

368 found that in three out of the four conditions the weight on the current hint in trial 11 is lower than

369 in trial 1. Only for the easy task difficulty level and the ordering of first anti-saccades and then

370 pro-saccades, the weight on the presented hint at trial 11 was as high as at the beginning of the

371 block (**Fig.6 C** red dashed line). Also inspired by the initial modeling results on participants'

372 strategies (**Fig.4**), we tested the influence of previous guesses further in the past (two trials (D)

373 and three trials (E)). Again, we found that there is no knowledge transfer across the response

374 switch. In summary, these results show that participants were unable to use their past estimates,

375 made with another response type, to inform their current guess.

376 One possible explanation for these results is that participants had difficulties in understanding that

377 the hidden target location had remained the same across first and second 10 trials (or between trial

378 10 to 11). To rule out this possibility, we performed a second experiment with an independent set

379 of participants (N=20) where we further emphasized that the target location was the same across

380 the two halves of the experiment. Furthermore, we asked the participants at the end of each block

381 whether they were aware that all twenty trials performed so far belonged to the same hidden target.

382 We obtained overall similar results in this experiment (**Fig. S3**), as learning performance, as well

383 as information transfer and confidence were disturbed after the response switch between trial 10

384 and 11, despite the fact that participants were explicitly instructed that all twenty trials belonged

385 to the same hidden target and that they were also aware of this rule (**Fig. S3 B**). This indicates that

16

386 the inability to transfer knowledge between response types is not because of a cognitive

387 misunderstanding of the task.

388
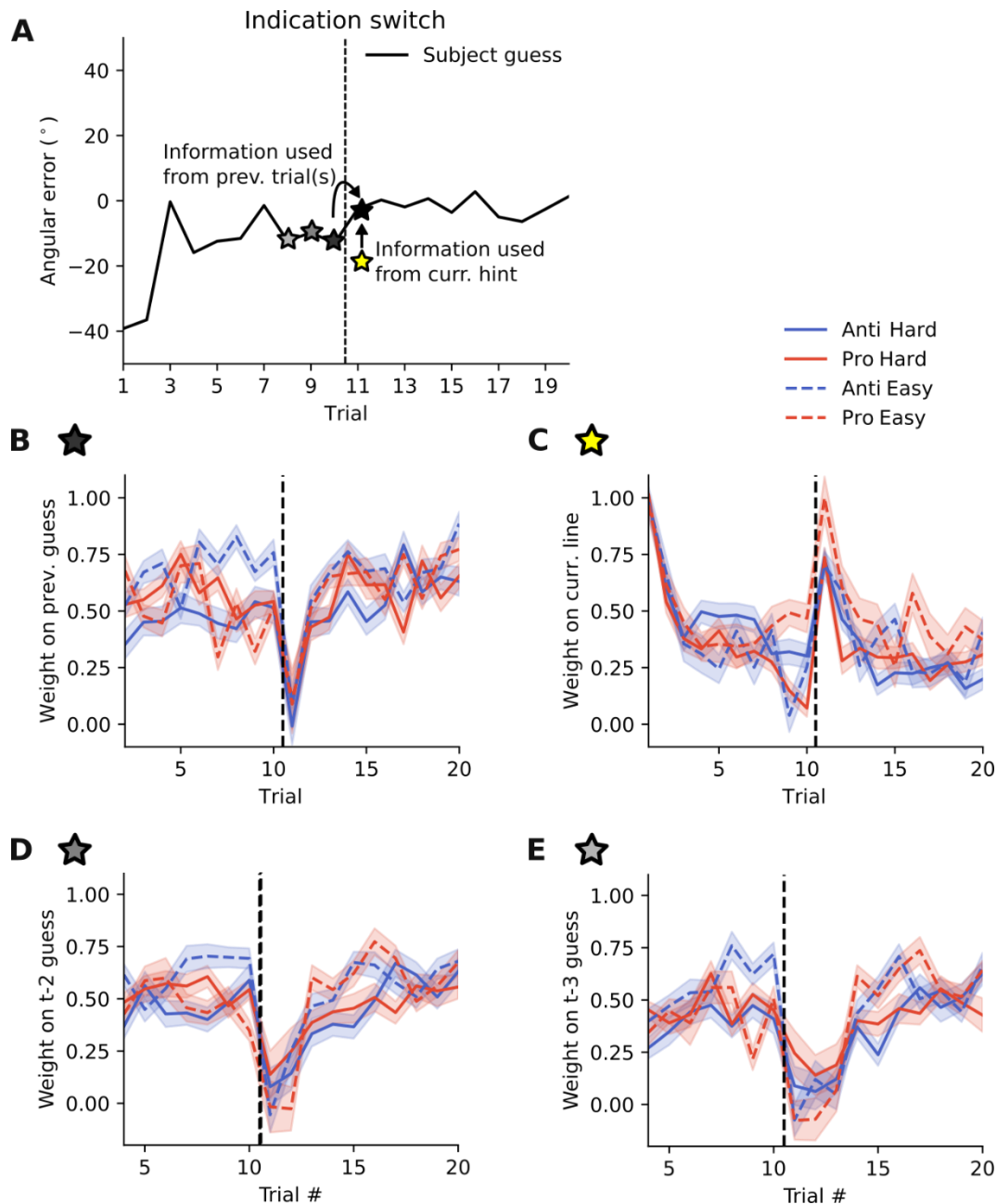
Figure 6: *No knowledge transfer between visuo-motor modalities.* (A) To test if there is any knowledge transferred from the experience with one response type to the other, we regressed the current guess against previous guesses/current hint. (B) Participants' estimates at trial 11 (after response switch) are independent of the estimates at trials 10 (before response switch). In contrast, at every other time point, participants use previous experience to inform their current guess. (C) At trial 11, participants highly rely on the information coming from the current hint. (D-E) Besides transfer from one trial to the next (B), there is also no transfer from trials further in the past across the response switch.

17

Discussion

The aim of the current study was to characterize the dynamics of prior learning and its dependence on the type of motor response used to report choices. We found that participants could learn a sensorimotor prior within a few trials, with the learning time course being independent of the response type (pro- or anti-saccades). By using a model-comparison approach, we further demonstrated that participants relied more on their own guesses from previous trials compared to visual hints provided in previous trials – again – independent of the response type. This suggests that prior knowledge is represented in terms of previous motor actions and not incoming, external information provided by the visual hints. To verify this hypothesis, we tested whether participants could generalize their learned prior knowledge from one motor context to the other – a switch from pro- to anti-saccades or vice versa. We found that switching the response type caused participants to reset to naïve levels of performance, indicating that experience from one response type could not be generalized to the other. This was the case even despite explicit instructions and participants' awareness that pro- and anti-saccade trials belonged to the same hidden target location. Our results suggest that humans learn sensorimotor priors through monitoring their previous motor decisions rather than external sensory hints. The dependence of learning on past motor decisions discourages generalization of the learned knowledge to conditions where a different visuo-motor mapping is needed.

Our findings suggest that prior knowledge is represented in a motor specific manner during early learning, which is in line with previous studies reporting motor specific priors in different paradigms [15,16]. We could furthermore identify one potential reason for why generalization is not possible in such contexts, as we found that participants do not memorize the external information from previous trials (visual hints in our case), but instead they memorize their own actions in each trial (**Fig.4 E-F**). As our task required an estimation in every trial, indicated by either a pro- or an anti-saccade, the memory of each trial's decision was probably represented as the motor action taken to indicate the guess. This could also explain why tasks which do not require an explicit response via a motor action are more generalizable [15]. In these cases, the memory from previous trials is potentially formed in a more abstract way, as participants only have to 'think' about their decision, but not perform any specific action. The finding that prior knowledge is built on internal decisions, compared to external cues, could therefore unify some previous controversial findings about prior generalization.

427   Despite the suggested motor specific formation of prior knowledge, the algorithm to combine
428   previous experiences to inform the current decision seemed to be similar for both tested response
429   contexts (**Fig.4 E-H**). This suggests that there is a general procedure for how humans combine
430   previous experiences. However, whether prior knowledge can generalize or not depends on the
431   specific manner through which previous experience or decisions are stored in memory (e.g., in
432   terms of motor actions or more abstract decisions). In other words, although at an algorithmic level
433   learning is independent of the response modality, the learned information is stored with a format
434   that is specific for each modality. This explanation is in line with the previously proposed
435   dissociation between learning a *policy* versus *knowledge* [16], and further narrows the space of
436   testable predictions regarding the neural implementation of these different types of learning, as the
437   well-described neuronal machinery of pro- and anti-saccades [18,19] could allow a
438   characterization of how the two types of learning occur in the brain, for instance through using
439   neuroimaging techniques.

440   Our study is different from previous studies as it does not test prior learning in a condition where
441   there is also sensory uncertainty [5,17]. In these general task designs, participants are asked to
442   perform a task trial-by-trial and are not explicitly told to combine information from previous trials.
443   Prior learning in these cases is therefore implicit and potentially unconscious. Furthermore,
444   learning is mostly observed by analyzing how participants combine the noisy sensory information
445   in a given trial with the formed prior. It is therefore not directly possible to resolve which of the
446   two is learned, as observed changes in this combination could potentially come from a changed
447   likelihood distribution, from a changed prior distribution, or from changes in both distributions.
448   Because of these limitations, we designed our task such that the sensory information in each trial
449   was given by a clearly visible hint. We then explicitly asked the participants to combine the
450   information across trials to find the hidden target location. Compared to previous prior learning
451   studies [5], we could therefore directly look at the ability to learn statistical regularities over trials.
452   This more general statistical learning context has also been studied previously, for example
453   showing that learning can happen rapidly within a dozen trials if feedback is provided [20].
454   However, to our knowledge, pure statistical learning, without trial-by-trial feedback, together with
455   generalization has not been studied in this context.

456   The two different task contexts we investigated in this work are distinct to previous studies, as we
457   did not test generalization from one effector to another, such as performing a task with the right

458   hand and switching to the left [11,21], or switching from a motor to a perceptual task [16]. Instead,

459   our two contexts represent two distinct cue-action mappings, though performed with the same

460   modality (oculomotor system). By cue-action mapping we mean that participants had to indicate

461   their guess (the internal cue) with two different response types – pro- and anti-saccades (the

462   actions), dependent on the task context. Potentially, generalization could be easier between

463   modalities compared to generalization between different cue-action mappings. Given the specific

464   design of our task, we cannot differentiate whether participants form a motor independent spatial

465   prior, which is aligned to the given cue-action mapping, or whether they form their prior directly

466   at the motor level. In both cases generalization would fail, matching our experimental observation.

467   Potentially, participants learn a spatial representation in the pro-saccade context, where the correct

468   estimate lies close to their performed motor action endpoint. Then, in the anti-saccade context,

469   they don't follow this estimate and solely invert their motor plan, but instead they form a 'pro'

470   representation of the hidden target location in this new context, where again the performed motor

471   action endpoint is close to the acquired spatial estimate. In this interpretation, anti-saccades are

472   not really anti-saccades, but pro-saccades relative to the participants' estimates and only visual

473   information is inverted. What speaks for this interpretation is the fact that participants seemed to

474   be closer to the optimal learning performance in the anti-saccade condition (**Fig.3 F-G**), although

475   this was only the case when the visual hints were narrowly distribution.

476   Our setup allowed us to simultaneously evaluate participants' performance, as well as their

477   confidence in their given estimation. Interestingly, confidence also decreased after the response

478   type switch, suggesting that participants were aware that they cannot generalize between both

479   contexts. On the other hand, a control experiment, where we explicitly asked participants to

480   indicate after each block whether they were aware that both response type contexts belonged to

481   the same hidden target estimation, showed that that they knew that information could be combined

482   across both contexts (**Fig. S3 B**). Together, these results suggest that participants' inability to

483   transfer knowledge from one response context to the other was not due to conscious

484   misunderstanding, but more likely due to the specific mechanisms of how the prior is formed

485   unconsciously.

486   Although our results, especially the inability to generalize across different motor contexts, suggest

487   that statistical learning is implemented in a low-level, motor-dependent way (**Fig.5&6**), there

488   might be potentially alternative explanations for why we could not see generalization in our

489   experiment. In the following we will discuss these alternative interpretations. One potential

490   explanation for the lack of generalization could be an interference between the internal memory of

491   the target location, which is disturbed by the information slide, presented between trial 10 and 11

492   indicating response switch (**Supplementary Video 1**). Another possibility is that the short

493   timescale of only ten trials is not enough to form a general representation of the estimated target

494   location. Potentially, initial learning is motor-dependent, but over time this is transformed to a

495   motor-independent knowledge, which can then be transferred to other motor contexts. Another

496   possibility is that participants would need to train on our task for more than one session, such that

497   they can learn to adapt their way of forming the prior to something which allows for generalization

498   across response contexts. Finally, one major reason for a motor-context dependent learning could

499   be that we did not provide external feedback to guide the learning process (unsupervised learning).

500   Instead, participants had to rely solely on their internal feedback, potentially coming from the

501   motor system. Future studies will be needed to test these possible explanations.

502   Spatially directed movements such as saccadic eye movements and reaching are an integral part

503   of our daily activities and acquired skills (e.g., imagine a cellist or a tennis player). Both types of

504   movements are profoundly influenced by statistical priors [1,22]. Furthermore, saccadic eye

505   movements provide detailed sensory information about a scene and are tightly linked to the

506   allocation of attention, hence being instrumental for active vision [23,24]. Typically, the effect of

507   statistical priors on saccadic eye movements is investigated by using a fixed set of potential target

508   locations, where the probability of target appearing in some locations (hence the uncertainty of

509   that location) is more than the others. The typical finding of these studies [22,25] is that saccade

510   latencies became shorter with increasing prior probability of the corresponding target location.

511   One novel aspect of the current study is to test how spatial priors can be learned through eye

512   movements under more complex settings where the possible target locations are not fixed, and

513   probabilities could only be inferred through tracking noisy information over time. In comparison

514   to the saccadic eye movement, reaching movements have enjoyed a more rigorous characterization

515   of the learning dynamics [5,12,14,16]. Inspired by these studies, we characterized the dynamics of

516   statistical learning through eye movements, that are a more accessible motor plan to be tested in

517   the laboratory, and the learned information acquired through their execution can directly impact

518   the very way that the brain samples the sensory information [26].

Materials and Methods

In this study, we report the results of two experiments investigating how a spatial prior is learned under different oculomotor response contexts. The second experiment was identical to the first and served as a control for ensuring that participants were aware of how the location of the learned prior varied across blocks of the experiment (see the description of the Experimental design). We therefore, describe the methods common to both experiments and mention the difference where they apply.

Participants

In total, 41 participants were recruited for this study. 21 participants (age range 22-38 years, M=26.05, SD=3.80, 10 females) took part in the first experiment. All participants had normal (N=9) or corrected-to-normal vision (N=12). One participant was excluded from the data of the first experiment as the post-experiment questionnaire indicated that the participant had misunderstood the task. 20 participants (age range 23-38 years, M=28.95, SD=5.07, 11 females) took part in the second experiment (with no exclusion) and all had normal (N=16) or corrected-to-normal vision (N=4). Participants were recruited from the general population of the city of Göttingen, Germany, using flyer and online advertisement and received cash financial compensation for their participation. Participation was voluntary; all participants were informed about the study procedure and gave written consent prior to the test session. The study was approved by the local ethics committee of the "Universitätsmedizin Göttingen" (UMG), under the proposal number 15/7/15.

Experimental setup

The stimuli were presented at the center of a calibrated ViewPixx/EEG monitor (VPixx Technologies, QC Canada, dimension: 53 x 30 cm, refresh rate: 120 Hz) with a resolution of 1920 x 1080 pixels at a viewing distance of 60 cm. All experiments were scripted in MATLAB, using Psychophysics toolbox [27]. Eye movements were measured using the Eyelink1000+ eye tracking system (SR Research, Ontario, Canada) in a desktop mount configuration, recording the right eye, with a sampling rate of 1000 Hz. A chin rest was used to stabilize the participant's head. The EyeLink camera was controlled by the EyeLink toolbox in MATLAB [28]. At the beginning of each experiment, as well as after every 10 blocks of the *Hidden Target Task* (see the Experimental design), the eye tracking system was calibrated using a 13-point standard EyeLink calibration procedure. Calibration was repeated until an average error of maximum 0.5 visual degrees was achieved and the error of all points was below 1. If the calibration accuracy dropped during the

551 experiment, e.g., due to the subjects' movement, the experimenter recalibrated the eye tracking

552 system again.

Experimental design

554 The experiment comprised two tasks: a calibration task (to estimate the motor error of pro- and

555 anti-saccades) and the main task, referred to as the 'hidden target task' (**Fig.1**). There were in total

556 four blocks of the calibration task (n=20 trials in each block) and forty blocks of the hidden target

557 task (n=20 trials in each block). Each experiment started with a block of the calibration task

558 followed by one training block for the hidden target task (n=10 trials in this block). The data from

559 this training phase was not analyzed. Thereafter, the experiment proceeded to the main task where

560 participants performed 10 blocks of the hidden target task followed by 1 block of the calibration

561 task. This sequence was repeated 4 times (**Fig.1 E**).

562 In a second experiment, we used the exact same experimental design but enforced the instruction

563 that the location of the hidden target remained the same across a block of 20 trials although the

564 response type changed halfway through (from anti- to pro-saccade or vice versa). For this, we

565 adapted the information slides shown during the experiment (**Supplementary Video 1&2**).

566 Furthermore, we asked the participants after every twenty trials of a hidden target whether they

567 were aware that the last twenty trials belonged to the same hidden target. Participants then had to

568 press a button to indicate their response, either yes or no.

Hidden Target Task

570 Participants were instructed to look for a 'hidden treasure' location on a ring with a radius of 7.5°,

571 centered in the middle of the screen (**Fig.1 A**). The word 'hidden treasure' was used in our

572 instructions to the participants to make the task more realistic and engaging, however we will refer

573 to the task as the 'hidden target' task throughout. Each trial started with a fixation period, where

574 participants had to fixate for 0.5 s on the white cross (size = 0.1875°, color: white, displayed on a

575 half-grey background) in the middle of the screen (**Fig.1 B**). After that, a white line (length =1.125,

576 color: white) was presented and participants had 3 s to estimate the hidden target location for this

577 trial and indicate their guess either by looking at it (pro-saccade) or by looking opposite of it (anti-

578 saccade) and fixate their estimated location for 0.5 s. Thereafter, participants rated their level of

579 confidence in their guess on an discrete scale from 1 to 6, where 1 means very uncertain and 6

580 means very certain about the target location. The confidence rating had to be done within 4

581 seconds.

Participants were told that they had twenty trials to guess the location of the hidden target, after which a new hidden target had to be found. To estimate the hidden target location participants had to closely monitor the location of a line that was presented in every trial and served as a visual hint. The hidden target location was the mean of a von Mises distribution and each visual hint was a sample drawn from this distribution (see below) [17]. Hence, by paying attention to the location of the hint across trials, participants were able to infer the underlying distribution of the hidden target location. Participants indicated their estimates by looking either at where they thought the hidden target was located on the ring (pro-saccade), or at a location directly opposite to it (anti-saccade). Ten consecutive trials of a block of twenty trials required pro-saccade responses, and the other ten anti-saccade responses. The type of the required response (either pro- or anti-saccade) was visually indicated by an instruction display presented every ten trials. Participants were instructed to perform the same type of response for ten trials in a row, until the response type changed.

In total, there were forty hidden target blocks. The target location of each block, which is the mean of the von Mises distribution, was randomly drawn from a fixed set of twenty locations evenly distributed on the circle. Thus, each location only appeared twice during the experiment. To familiarize the participants with the connection between the hints and the hidden target location, ten training trials were performed in the beginning of each experiment. After the ten training trials, participants saw all the ten lines together on the screen, as well as the correct hidden target location. Furthermore, after each hidden target block, participants saw where the actual hidden target location was, but they did not receive feedback about their performance on a trial-by trial basis. As such, in our experiments learning was unsupervised.

Four different experimental conditions, counter-balanced across blocks, were tested. Each block was either *easy* or *hard*, controlled by adapting the concentration of the von Mises distribution, and either ordered with first pro-saccade then anti-saccade, or first anti-saccade then pro-saccade response (**Fig.1 F**). For the easy task condition the concentration of the von Mises distribution (defined by κ which is a measure of dispersion, where $1/κ$ is equivalent to the variance σ^2_{dist} of the distribution) was 30 ($\sigma_{dist}\sim10°$), for the hard task condition it was 5 ($\sigma_{dist}\sim26°$) and for the training it was 80 ($\sigma_{dist}\sim6°$). As the concentrations of these distributions are relatively large, we could treat the von Mises distribution as a normal distribution and use standard statistics.

Calibration Task

The aim of this task was to quantify the participant-specific motor error of the visually-driven pro- and anti-saccades. Each block of this task consisted of twenty trials, from which the first ten were pro-saccades and the last ten were anti-saccades. On each trial, one out of ten equally distributed locations on the circle (same circle as in the hidden target task) were selected and a target line was presented at that location (**Fig.1 C**). Participants were instructed to look either directly at the displayed line (pro-saccade in the first ten trials), or directly opposite to where it appeared (anti-saccades, second ten trials). Additionally, it was highlighted that this task is completely independent of the hidden target task. Each trial consisted of an initial fixation phase, where participants had to fixate on the white cross in the middle of the screen for 0.5 s. After that, a white line appeared and participants had to either look at it or opposite of it (**Fig.1 D**). In the beginning of a block of ten trials, participants received an instruction display indicating whether they had to perform pro- or anti-saccades during the upcoming trials.

Successful response

For both tasks, a successful response was defined as follows. Participants had to move their gaze from the central fixation point towards a peripheral location on the ring. As soon as they moved away from the fixation and crossed a circular threshold of 5.375° a successful response was possible. To complete the response, participants furthermore had to fixate on one specific point on the screen, by holding their gaze for 0.5 s within an area with a radius of 1 .

Analysis

Data pre-processing

The recorded raw eye movement data was transformed to MATLAB files by using a MATLAB library for eye movement analysis [29]. Participants' estimates in each trial were calculated offline by averaging the eye movement data of the last 100 ms, out of the total 500 ms necessary for a successful response. The main eye movement parameter that we analyzed was the angular distance between the participant's estimate and the true hidden target location (**Fig.2 A**). Failed trials were excluded from the analysis. A trial could fail in several ways. Firstly, there could have been a disturbance with the eye tracking system or the participant's calibration so that the gaze position was not correctly detected, which made it necessary to re-calibrate the eye tracker. Secondly, the participant could have been too slow to indicate their guess in time (3 s). Thirdly, to exclude erroneous pro- instead of anti-saccades and vice versa, we analyzed the distribution of angular errors and found a bimodal distribution (**Fig. S4**). We set a threshold at 100°, which separated both

644 modes (**Fig. S4**). Thus, every trial with an absolute angular error bigger than 100° was categorized

645 as failed because of the wrong response type.

Data analysis

647 Statistical analyses were done using R and Python. To evaluate learning we used paired, two-sided

648 t-tests to compare several parameters within a participant. We did not use circular statistics as

649 subjects' responses where highly localized on the ring (**Fig.2 A-B & S4**). Learning was assessed

650 by measuring the decrease in the absolute angular error between the participant's estimate and the

651 true hidden target location across trials. Given the assumptions that the participant's estimates are

652 normally distributed and centered around zero, the mean absolute angular error can be related to

653 the variance of the Gaussian distribution by:

654 $\quad$ 2) $\; Mean(|x|) = \sqrt{\dfrac{2}{\pi}} \, SD(x)$

655 To compare the performance difference between pro- and anti-saccades, we calculated a 'modality

656 difference index' (**Fig.3 C**). For this, we first calculated the median of the absolute angular error

657 for pro-saccade and anti-saccade response trials. The modality difference index is then given by

658 the difference between the two medians, divided by their sum. We started our analysis by only

659 using the data from the first ten trials of each block (**Fig.1-4**). Only when we looked at the transfer

660 between modalities, we used all twenty trials of each block (**Fig.5-7**).

Theoretical bounds for learning performance

662 To evaluate participants' performance, we computed the theoretical lower bounds on the absolute

663 angular error they could potentially achieve by using all the information that was available to them.

664 Participants could use the previously seen visual hints and their memory of their previous motor

665 actions (referred to as the previous guess) to infer the most probable location of the target on each

666 trial. These sources of information are error-prone since on each trial participants had only seen a

667 limited number of visual hints (i.e., sampling error) and their previous responses contained motoric

668 noise. We assumed that these two sources of error are independent. The error due to the limited

669 number of visual hints was calculated as the cumulative mean of all hints seen so far, which

670 represents an optimal way of combining samples over time to estimate the mean of a distribution.

671 A constant motor error, measured for each participant during the calibration task, was used to

672 represent the motoric noise. The variance of the joint estimate, derived from combining visual

673 hints and motor actions, was then calculated by adding the variance of the two sources, based on

674   the assumption of their independence (cf. Eq.1). In addition, we also calculated a suboptimal,

675   'limited memory' lower bound to account for the information loss across time. This model makes

676   use of the latest two visual hints, instead of all, to infer the statistical distribution of the target. To

677   understand how participants used these sources of information to make decisions on a trial-by-trial

678   basis, we employed a detailed model-comparison approach as described below.

Modeling participants' behavior

679

680   We used linear regression models to analyze the single subject behavior. Four potential strategies

681   we wanted to test were: 1) looking directly at the visual hints in each trial, 2) estimating the

682   cumulative average of all visual hints so far, 3) looking at the same location as in the previous trial,

683   4) estimating the cumulative average of all previous guesses (as given by their saccadic responses)

684   (**Fig.4 A**). Strategy (2), calculating the cumulative average of all hints seen so far is directly linked

685   to the lower bound on performance described above. This is an optimal statistical strategy to

686   combine all observed hints and therefore produces the optimal performance. In principle, strategy

687   (2) is also equivalent to a Bayesian optimal strategy, as in our case each hint has objectively equal

688   certainty and should therefore be weighed equally.

689   We started with the four described single predictor models to see which of the four mentioned

690   strategies best describes participant's behavior. The dependent variable was the angular error of a

691   participant's estimate in a certain trial. The independent variable was the angular error of the

692   estimate, given by one of the above-mentioned strategies. Only the data from trial 4 onward was

693   included to test all models on the same data, since we wanted to test the influence of up to three

694   trials in the past on the current trial. In a second stage, we tested linear regression models with

695   multiple independent variables. We included previous guesses from up to three time steps in the

696   past, as well as the visual hints from the current and up to three time steps in the past. Each of the

697   described regression models was fitted to the single subject data. To compare these models, we

698   calculated BIC, delta BIC, and Bayesian weights [30], to assess the likelihood of each model being

699   the best fit to the data (cf. Evaluating model performance). Since these values are normalized, they

700   can be used to determine the model that on average best fits the participants' data.

Evaluating model performance

701

702   To compare the different linear regression models presented above we used a model comparison

703   evaluation based on Bayesian weights [30]. For this, we firstly calculated BIC values for each

704   model. Each BIC value was rescaled by calculating ΔBCI, which is calculating the difference to

705   the smallest BIC value in the group of models considered. This forces the best model to have

706   ΔBCI=0 and the other models to have positive values. We then calculated Bayesian weights ω

707   with:

708   3) $\omega_i = \frac{e^{-0.5\Delta \text{BIC}_i}}{\sum_{n-1}^{N}(-0.5\Delta \text{BIC}_n)}$

709   The Bayesian weights of all tested models in **Fig.4 B** sum up to 1 and define the probability of

710   being the best model, among the one tested.

711

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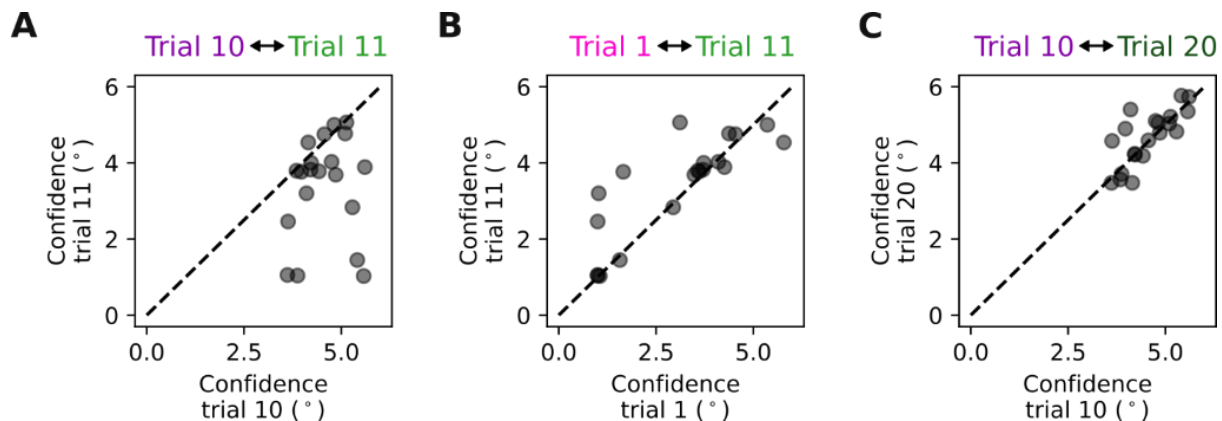781   doi:10.1177/0049124104268644

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Supplementary figures
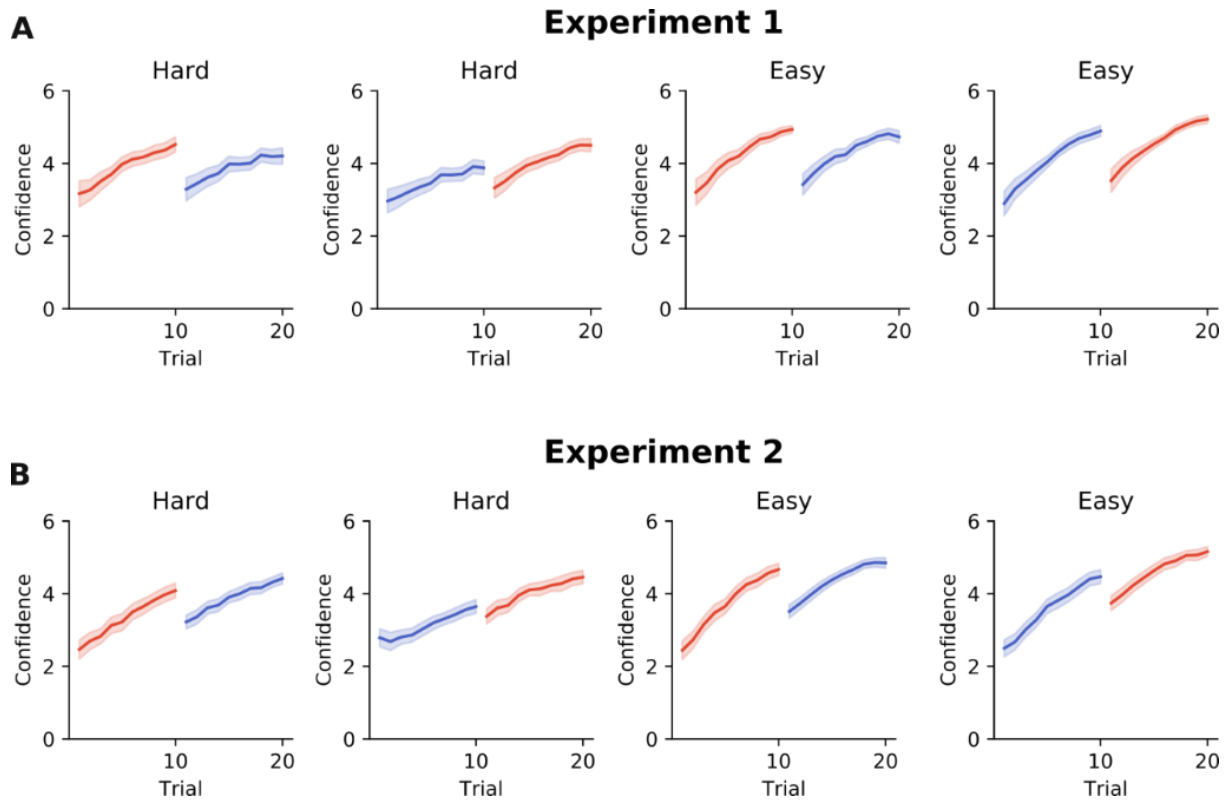
Figure S1: *Confidence time course.*

**Figure S2:** *Confidence drops after response switch.*

Figure S1 and S2 are supplementary to Fig.5 in the main text. The confidence ratings demonstrated the same results as observed by analysing the absolute angular errors of the eye movements, as there was a decrement in confidence between trials 10 and 11 as shown in S1-A) for Experiment 1, as well as in S1-B) for Experiment 2, for all experimental conditions. The drop in confidence between trial 10 and 11 was significant (S2-A). The confidence of trial 11 was not different from trial 1 (S2-B), and the last trial of a block of 20 trials was not significantly better than trial 10 (S2-C). These results support the observation that after a switch in response modality, learning starts from a naïve level.
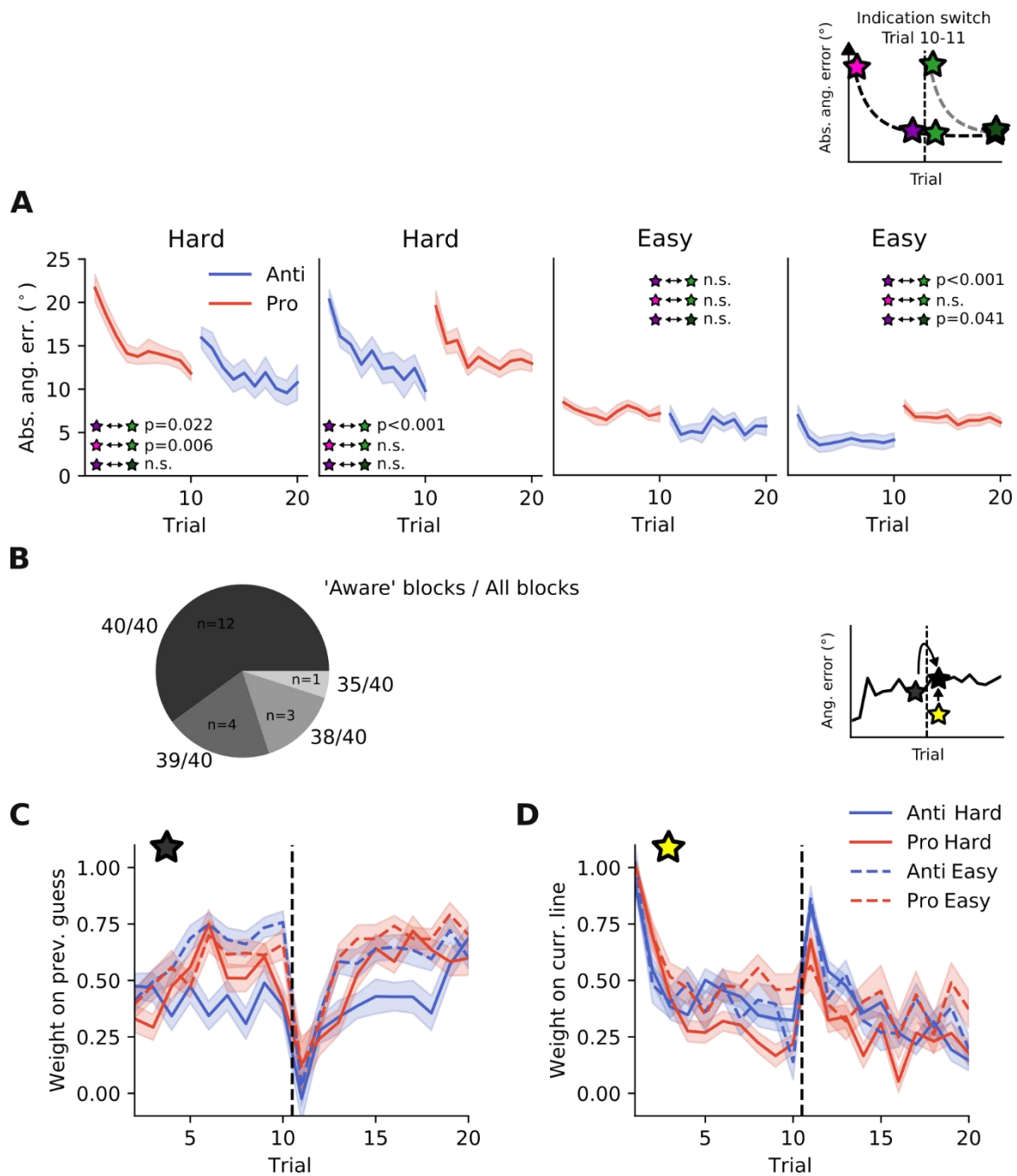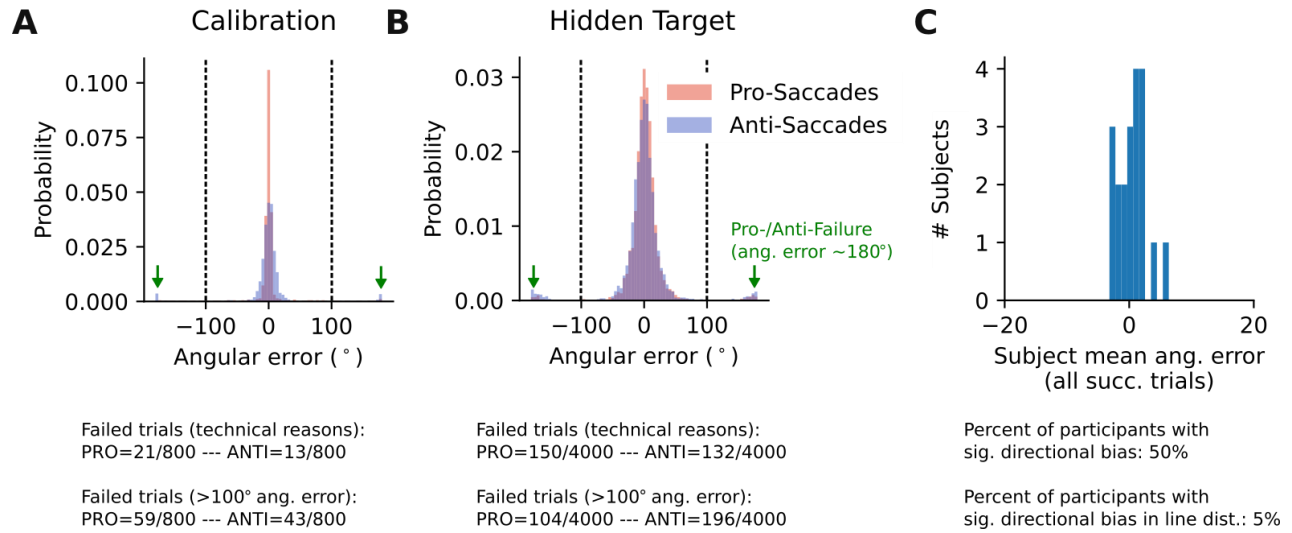
Figure S3: *Second experiment with reinforced instructions shows similar results.*

This figure is supplementary to Fig.5 and Fig.6 in the main text. These results demonstrate that we obtained similar results, when participants were explicitly instructed that the location of the hidden target remains the same after a switch. Additionally, participants had to report whether they were aware of this rule, thus reinforcing the instructions. A) Also in this experiment, performance dropped to naïve levels after a switch in response type. B) The majority of participants reported to be aware of the rule. C) The weighting of previous guesses dropped between trial 10 and 11 (when the switch occurred) and D) instead more weight was put on visual hints.

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Failed trials (technical reasons):
PRO=21/800 --- ANTI=13/800

Failed trials (>100° ang. error):
PRO=59/800 --- ANTI=43/800

Failed trials (technical reasons):
PRO=150/4000 --- ANTI=132/4000

Failed trials (>100° ang. error):
PRO=104/4000 --- ANTI=196/4000

Percent of participants with
sig. directional bias: 50%

Percent of participants with
sig. directional bias in line dist.: 5%

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816 **Figure S4:** *Threshold for failed pro-/anti-saccades and subject-wise directional bias.*

817 This figure is supplementary to Fig.3 in the main text. It demonstrates the rationale for excluding erroneous pro- and
818 anti-saccades. A) Data of Calibration Task. B) Data of Hidden Target task. In both panels, subjects' estimates are
819 shown without excluding 'wrong' saccades due to pro-/anti-saccade error. As shown in A and B, there is a bimodal
820 distribution of angular errors, especially in the hidden target task. The peaks at ±180° error represents the failed pro-
821 /anti-saccades, meaning trials where pro-saccades should have been made but the subject responded with anti-saccades
822 and vice versa. We set a threshold at 100 degree to distinguish correctly aimed pro- or anti-saccades. C) Distribution
823 of the mean angular error across participants indicates that there was no directional (CCW or CW) bias.

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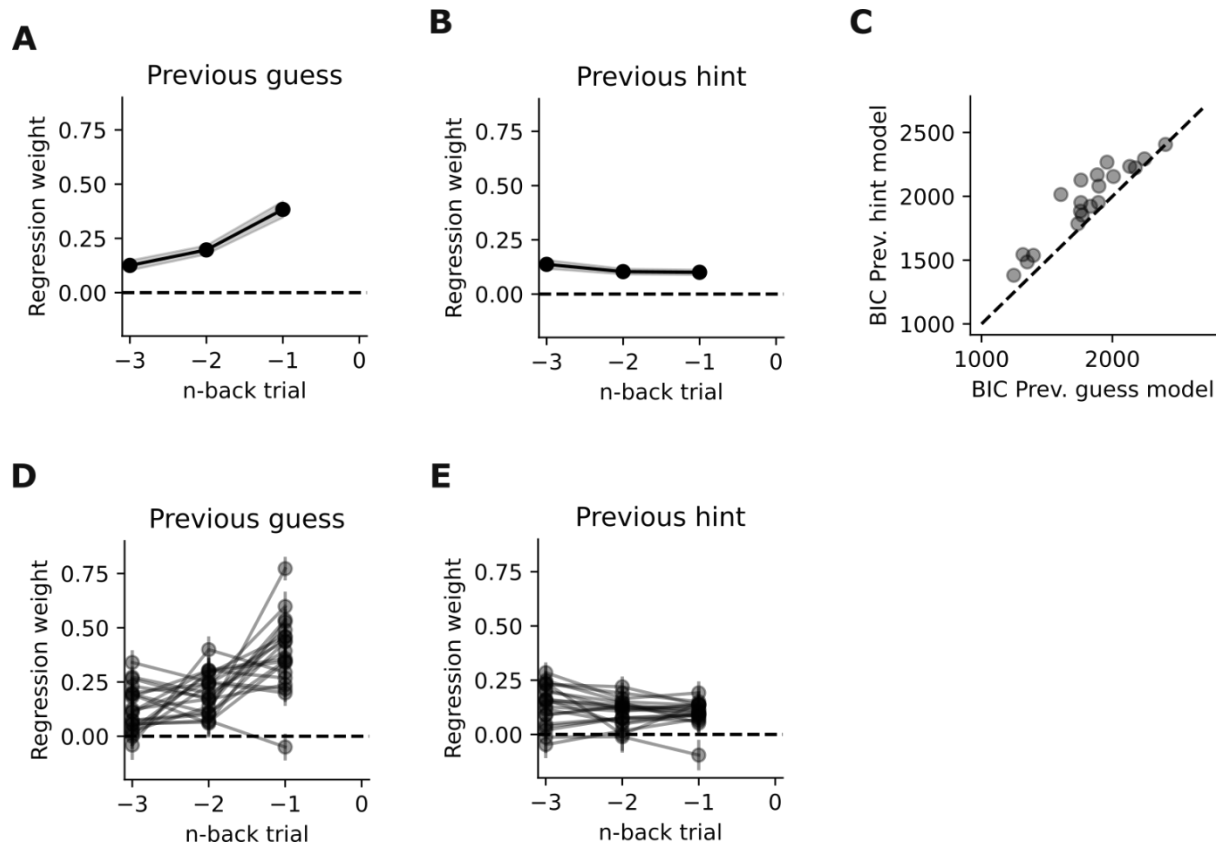
Figure S6: *Memory traces for previous guesses and hints.*

This figure is supplementary to Fig.4 in the main text. Here, we quantified how much weight is put on previous hints or guesses, tested in separate models each including either only the guesses or only the visual hints. A) Regression weights of the model including previous guesses as a predictor B) Same as A for a separate model including visual hints as a predictor 3) comparison of the model shown in A against the model shown in B. It can be seen that the previous guess models consistently outperformed the visual information/hints models, confirming the finding that subjects' behavior is better predicted by previous actions than external visual information D&E) Same as A&B, but showing the single subject regression weights instead of the average weights.