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Passive motor learning: Oculomotor adaptation in the absence of behavioral errors

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Passive motor learning:

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Oculomotor adaptation in the absence of behavioral errors

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Abstract

Motor adaptation is commonly thought to be a trial-and-error process in which the accuracy of movement improves with repetition of behavior. We challenged this view by testing whether erroneous movements are necessary for motor adaptation. In the eye movement system, the association between movements and errors can be disentangled, since errors in the predicted stimulus trajectory can be perceived even without movements. We modified a smooth pursuit eye movement adaptation paradigm in which monkeys learn to make an eye movement that predicts an upcoming change in target direction. We trained the monkeys to fixate on a target while covertly, an additional target initially moved in one direction and then changed direction after 250 ms. The monkeys showed a learned response to infrequent probe trials in which they were instructed to follow the moving target. Further experiments confirmed that probing learning or residual eye movements during fixation did not drive learning. These results show that motor adaptation can be elicited in the absence of movement and provide an animal model for studying the implementation of passive motor learning. Current models assume that the interaction between movement and error signals underlies adaptive motor learning. Our results point to other mechanisms that may drive learning in the absence of movement.

Significance statement

What are the signals that drive learning? Many experimental and theoretical studies have approached this question from the perspective of motor adaptation as it is both extremely relevant to everyday life and allows for tight experimental control. Motor adaptation is thought to be a gradual process in which errors in behavior are corrected. Here we challenged this view and developed a behavioral paradigm for studying whether movement is necessary for motor adaptation. We found that motor adaptive learning can be elicited in the absence of movement, thus suggesting that motor adaptation has a crucial passive component.

111 **Introduction**

112 To better understand learning, the signals that drive learning need to be identified
113 behaviorally to reveal their implementation at the neuronal level. Here we use the
114 characterization of motor adaptation as a gradual improvement in performance in response to
115 altered conditions (Krakauer and Mazzoni 2011). Motor adaptation is an especially valuable
116 model for studying learning since experiments can reproducibly generate perturbation and
117 then track the changes in behavior on a trial-by-trial basis. Recent research has highlighted
118 the importance of sensory feedback on movement in driving motor adaptation. For example,
119 the difference between the predicted and actual consequences of movement was shown to
120 have both a computational advantage and account for behavioral results (Shadmehr et al.
121 2010; Wolpert and Miall 1996). However, feedback on movement is only one of many
122 signals that may drive motor learning (Mazzoni and Krakauer 2006; McDougle et al. 2016;
123 Mostafa et al. 2019).

124 In terms of implementation, it has been hypothesized that in the cerebellum,
125 movement and sensory signals converge to drive adaptive motor learning (Wolpert et al.
126 1998). When an erroneous motor command is executed, the climbing fiber input to the
127 cerebellum drives plasticity that results in a more accurate upcoming movement (Gilbert and
128 Thach 1977; Ito 1982; Stone and Lisberger 1990). In the eye movement system, there is
129 impressive trial-by-trial evidence for an association between climbing fiber input (manifested
130 as complex spikes), the simple spike output of the Purkinje cell, and learned behavioral
131 changes (Herzfeld et al. 2018; Medina and Lisberger 2008; Suvrathan et al. 2016). In
132 addition, in the eye movement system there are extensive data showing which cerebellar sites
133 drive eye movement and the pathways that provide signals to these areas (Voogd et al. 2012).
134 Identifying non-motor signals in oculomotor learning can be interpreted in the context of
135 what is already known about the implementation of motor learning and lead to testable
136 hypothesis on where and how non-motor signals drive learning. Thus, we aimed to use an eye
137 movement adaptation paradigm, in which a link between learning and its implementation has
138 been established, to test whether movement is necessary for motor adaptation.

139 We modified a smooth pursuit eye movement learning paradigm to test whether
140 sensory feedback on eye movements is needed for learning to occur. When monkeys are
141 trained to track a moving target that repeatedly undergoes the same change in direction at a
142 predictable time, a learned smooth pursuit eye movement is elicited prior to the change in
143 target direction (Joshua and Lisberger 2012; Medina et al. 2005). These behavioral changes
144 occur quickly and reach near asymptotic values after 50 trials (Hall et al. 2018). During the
145 learning of perturbed target motion, the relationship between movement and prediction target
146 trajectory can thus be teased apart because motion can be sensed covertly without eye
147 movement. We therefore designed a new paradigm in which monkeys learned to predict a
148 change in direction of a target without tracking it. We termed this *passive motor learning*. We
149 examined this type of learning in infrequent trials in which monkeys tracked a moving target,
150 to show that monkeys can learn passively by observing and not tracking target motion. The
151 interpretation of these results, together with what we already know about the pursuit system
152 suggest testable hypotheses with respect to the areas and mechanisms involved in passive
153 motor learning.

154 **Methods**

155 We collected behavioral data from two male and two female *Macaca Fascicularis*
156 monkeys (4-6 kg). All procedures were approved in advance by the Institutional Animal Care
157 and Use Committees of the university and were in strict compliance with the National
158 Institutes of Health Guide for the Care and Use of Laboratory Animals. We implanted head
159 holders to restrain the monkeys' heads in the experiments. After the monkeys had recovered
160 from surgery, they were trained to sit calmly in a primate chair (Crist Instruments) and
161 consume liquid food rewards (baby food mixed with water and infant formula, 0.1 mL /trial)
162 from a tube set in front of them. We trained the monkeys to track spots of light that moved
163 across a video monitor placed in front of them.

164
165 Visual stimuli were displayed on a monitor 65 cm from the monkeys' eyes. The
166 stimuli appeared on a dark background in a dimly lit room. A computer performed all real-
167 time operations and controlled the sequences of target motion. The position of the eye was
168 measured with a high temporal resolution camera (1 KHz, Eye link - SR research) and
169 collected for further analysis. Monkeys received a reward when tracking the target
170 successfully.

171
172 Pursuit stimuli were presented in trials. In the eye movement trials, each trial started
173 with a circular white target that appeared in the center of the screen. After 1s of presentation,
174 in which the monkey was required to acquire fixation ($3 \times 3^\circ$ window), the target began
175 moving. The exact target trajectory is detailed below according to the different blocks. The
176 monkeys were rewarded at the end of trials for keeping their eyes within a window of $5 \times 5^\circ$
177 around the target. We used a large fixation window so that the monkeys' behavior was not
178 restricted during the learning trials. In the fixation trials, two targets were displayed: a
179 stationary and a moving target. The stationary target was a 1° side length square which was
180 displayed during the entire trial. The moving target was a white circular spot (except on
181 reward blocks, see below), similar to the target on the eye movement trials. At the beginning
182 of each trial the stationary target appeared in the center of the screen and the monkey was
183 required to acquire fixation ($3 \times 3^\circ$ window). After 1 second, the moving target appeared and
184 started to move with a trajectory that varied depending on the block. To be rewarded, the
185 monkey had to keep its gaze on the stationary target. To keep conditions similar in the eye
186 movement and fixation trials we used the same size fixation window as in the eye movement
187 trials. We verified the potential confound that the monkeys might initially track the moving
188 target although they were instructed to fixate. We confirmed that the monkeys only made
189 very small eye movements during the fixation trials and we designed experiments to control
190 for this movement (see below, paradigm 3). Trials were considered to have failed if the
191 monkey interrupted fixation at any step during the trial. After a failed trial, the same trial was
192 presented to the monkey until success.

193 The paradigms consisted of learning blocks interleaved with washout blocks (if not
194 specified otherwise). Each block consisted of 100 successful trials. We detail the composition
195 of the different learning blocks below. Washout blocks consisted of 50 eye movement trials
196 and 50 fixation trials interleaved randomly in which after 1 second, the moving target stepped
197 to a 4° eccentric position and started to move in the opposite direction at $20^\circ/\text{s}$ (step-ramp,
198 Rashbass and Westheimer, 1961). The target continued to move for 650 ms after motion
199 onset and then stopped and stayed still for an additional 500 ms.

200 *Paradigm 1: Motor blocks, fixation congruent and incongruent blocks*

201 The motor blocks consisted of 100 eye movement trials in which the target moved
202 initially in one direction and then after 250 ms, an orthogonal 20 °/s component of motion
203 was added (Medina et al. 2005). We term the direction of the initial target motion and the
204 direction of the orthogonal component the *base* and *learned* directions. To select the learned
205 direction, we prescreened the monkeys' behavior to select target motion directions in which
206 we could consistently drive learning. Specifically, these directions consisted of down and
207 rightward for the base and learned directions.

208 The fixation congruent and incongruent blocks consisted of 90 fixation trials and 10
209 eye movement trials. In the fixation congruent blocks, the moving target changed direction
210 (the same as for trials in the motor learning block). In fixation incongruent blocks the moving
211 target did not change direction (similar to trials in the washout blocks). In the eye movement
212 trials in both fixation blocks (congruent and incongruent) the target changed direction (same
213 as in trials in the motor learning blocks). In both types of fixation blocks, each group of 10
214 trials included 9 fixation trials and 1 eye movement trial introduced randomly between them.
215 Motor, congruent and incongruent blocks were randomly interleaved and separated by
216 washout blocks. The average learned response at the end of the washout blocks (25 last eye
217 movement trials) was defined as the baseline level. We recorded this paradigm for 7 days for
218 each monkey which typically consisted of 9 learning blocks (3 of each type) and 9 washout
219 blocks.

220 *Paradigm 2: Fixation blocks without change in direction in eye movement trials*

221 In this paradigm we compared two types of fixation learning blocks. The first learning
222 block consisted of 90% of fixation trials in which the moving target changed direction. In the
223 following learning block the learning direction was rotated 180°. In both blocks, in eye
224 movement trials (10%), the target did not change direction (same as for trials in the washout
225 blocks). We recorded this paradigm for 3 days for each monkey which typically consisted of
226 24 learning blocks (12 of each type). In this paradigm we directly compared adjacent blocks
227 with opposite learning direction; therefore, we did not need to introduce washout blocks to
228 assess learning.

229 *Paradigm 3: Small angle and no angle blocks*

230 In this paradigm we compared two blocks that only included eye movement trials. In
231 the no angle blocks, in most trials (90%) the target did not change direction (same as for trials
232 in the washout blocks). In the small angle blocks, in most trials (90%) the target changed
233 direction 250 ms after motion onset (as in the motor blocks) but the velocity component in
234 the learned direction was only 0.5°/s. In the two blocks, learning was assessed using eye
235 movement trials (10%) in which a 20 deg/s orthogonal component was added after 250 ms of
236 target motion (same trials as in the motor blocks). We recorded this paradigm for 3 days for
237 each monkey which typically consisted of 12 learning blocks (6 of each type) and 12 washout
238 blocks.

239 *Paradigm 4: Motion and position blocks*

240 In this paradigm, we compared two learning blocks, the motion blocks were similar to
241 the fixation congruent blocks in which during fixation (90%) and the movement trials (10%)
242 the moving target changed direction. In the position blocks during the fixation trials (90%)
243 the moving target vanished at the change in direction (250 ms after motion onset) and
244 reappeared at the end of motion (650 ms after motion onset). The remaining 10% were eye

245 movement trials in which the target changed direction. We recorded this paradigm for 3 days
 246 for each monkey which typically consisted of 12 learning blocks (6 of each type) and 12
 247 washout blocks.

248 *Paradigm 5: Congruent rewarded block and incongruent rewarded block*

249 In this paradigm, we compared two learning blocks with two types of fixation trials
 250 (45% each) and eye movement trials (10%). In both blocks, the moving target changed
 251 direction in half of the fixation trials and did not change direction in the remaining trials. In
 252 the congruent rewarded blocks, the monkey was only rewarded when the moving target
 253 changed direction. In the incongruent rewarded blocks, the monkey was only rewarded when
 254 the moving target did not change direction. The color of the moving target signaled the
 255 presence of reward. In the rewarded fixation trials, a green moving target was used for
 256 Monkey C (blue for Monkey A) and an orange target for non-rewarded trials (pink for
 257 Monkey A). Monkeys were familiar with the color-reward association as we used the same
 258 monkeys with the same associations in prior studies (Larry et al. 2019; Lixenberg et al.
 259 2020). The eye movement trials (10%) were identical to those described in the motor blocks
 260 (with a regular white target). We recorded this paradigm for 3 days for each monkey which
 261 typically consisted of 12 learning blocks (6 of each type) and 12 washout blocks

262 *Paradigm 6: Learning with multiple base and learned directions*

263 In this part of the experiment, we compared fixation congruent and motor blocks
 264 when we interleaved blocks with many base ($0^\circ, 90^\circ, 180^\circ$ or 270°) and learned (clockwise
 265 and counter clockwise) directions. Blocks were selected pseudo-randomly such that all the
 266 directions had to be selected once before any direction was selected another time. Learning
 267 blocks were interleaved with washout blocks where the base direction was similar to the base
 268 direction in the subsequent learning block. We recorded data for 8 days for each monkey,
 269 which resulted in 4 motor and fixation blocks in each direction.

270 Paradigms 1-5 were administered to two monkeys (A and C) whereas paradigm 6 was
 271 administered to the other two monkeys (E and F).

272 *Data analysis.* Learned velocity was computed as the velocity in the learned direction
 273 minus the average eye velocity of the last 25 eye movement trials in the corresponding
 274 washout blocks. The learned response was computed as the average learned velocity during
 275 the 100 ms around the change in direction in eye movement trials. We adjusted the signs of
 276 the data such that positive values of learning indicate eye velocity in the learning direction.
 277 We estimated the growth of learning (L) over trials by fitting the sum of two exponentials to
 278 the learned responses.

$$L = A_1(1 - e^{(-T/\tau_1)}) + A_2(1 - e^{(-T/\tau_2)})$$

279 where A_x is the peak magnitude of learning, τ_x is the “time constant” of learning, and $T+1$ is
 280 the trial number.

281 We used eye velocity and acceleration thresholds to detect saccades automatically and
 282 then verified the automatic detection by visual inspection of the traces. The velocity and
 283 acceleration signals were obtained by digitally differentiating the position signal after we
 284 smoothed it with a Gaussian filter with a standard deviation of 5 ms. Saccades were defined
 285 as an eye acceleration exceeding $1000^\circ/s^2$, an eye velocity crossing $15^\circ/s$ during fixation or
 286 eye velocity crossing $50^\circ/s$ while the target moved. We first removed the saccades and treated
 287 them as missing data. We then averaged the traces with respect to the target motion onset.

288 Finally, we smoothed the traces using a moving average filter with a span of 21 ms.

289 To calculate the ratio between the learned response in the motor to other blocks, we
290 first computed the averaged learned response across monkeys and trials in eye movement
291 trials in the motor, congruent fixation and incongruent fixation blocks. Then, we divided the
292 average learned response of the corresponding block by the average learned response in the
293 motor blocks.

294 **Results**

295 Learning to predict changes in target direction by observation

296 We used a smooth pursuit eye movement learning paradigm in the monkeys (Fig. 1A
297 and B), to test whether feedback on behavioral errors was needed to adjust behavior. The first
298 step consisted of a motor learning block (Joshua and Lisberger 2012; Medina et al. 2005)
299 where the monkeys tracked a single moving target that changed direction 250 ms after the
300 onset of motion (Fig. 1A top, *eye movement trial*). We term the direction in which the target
301 initially moved the *base direction* (downward in Fig. 1A) and the orthogonal direction in
302 which we later added a velocity component the *learned direction* (rightward in Fig. 1A). In
303 the initial learning trials, the eye movement in the learned direction was reactive rather than
304 predictive. After the target changed direction, the eye moved abruptly with a visually driven
305 characteristic reaction time (about 100ms, Fig. 1C gray line). After several repetitions of
306 trials with a change in direction the monkeys learned to predict the upcoming motion and
307 moved their eyes in the learned direction even before the target changed direction (Fig. 1C
308 black line, arrow points to the learned component). In this paradigm the predictive eye
309 velocity was not sufficient to completely match the upcoming target motion, so that the
310 monkeys still abruptly responded to the change in direction (Fig. 1C, black line) which was
311 often followed by a catchup saccade (not shown). To avoid confounding the learned with the
312 visually driven response, the analysis here was restricted to the first 300 ms after motion
313 onset in the base direction (Fig. 1D and E).

314 Theories of motor learning often assume that sensory feedback on movement errors in
315 learning trials drives subsequent learning (Ito, 1972; Ito and Kano, 1982; Wolpert, 1998). To
316 test whether the feedback on eye movement is necessary for learning, we designed an
317 additional learning block, termed the fixation block, in which the target changed direction,
318 but the monkey did not follow it. In most trials (90%) the monkeys were required to maintain
319 fixation on a square in the center of the screen while the moving target changed direction
320 (Fig. 1B). Unlike the eye movement trials, in the fixation trials the monkeys were passive:
321 they fixated the center of the screen, which prevented them from tracking the moving target
322 and responding to the change in motion direction.

323 We tested learning in a small fraction of trials (10%) in which the square fixation
324 target was not displayed, and the monkeys were required to follow the moving target exactly
325 as in the eye movement trials (Fig. 1A). In these trials, the monkeys shifted their gaze in the
326 direction of motion even before the target changed direction (Fig. 1D, gray solid trace). To
327 assess whether the monkeys indeed learned from these fixation trials we compared the
328 learned response in the fixation blocks to the end of the washout blocks. The washout blocks
329 consisted of 100 trials in which the target never changed direction (see Methods). By the end
330 of the washout block (termed baseline trials), the eye velocity in the learned direction was
331 close to zero (Fig. 1D, dashed trace). We quantified the learned response as the average eye
332 velocity in the learned direction between 200 and 300 ms after motion onset. The learned

333 response was maximal for the motor learning blocks, intermediate in the fixation blocks, and
334 the smallest in the washout blocks (Friedman test, $p = 10^{-12}$, post-hoc signed rank test with
335 Bonferroni correction, motor > fixation $p = 1.2 \times 10^{-9}$, fixation > washout, $p = 2.5 \times 10^{-9}$, $n = 46$).
336 As expected, there were only very minor difference between these three conditions in the
337 base direction (Fig 1E), indicating that the learned response indeed reflected a change in eye
338 movement direction and not an overall gain (Hall et al. 2018). Thus, in sessions with
339 infrequent eye movement trials, the monkeys adjusted their behavior to the change in target
340 motion, suggesting that learning was acquired in fixation trials without movement.

341 *Movement in infrequent trials does not explain the learned response in fixation blocks*

342 Next, we ruled out the possibility that learning in fixation blocks was driven solely by
343 the infrequent trials (10%) in which the monkeys tracked the target. We tested the behavior of
344 the monkeys in additional learning blocks in which the target did not change direction on the
345 fixation trials (Fig. 2A). We termed these blocks *incongruent learning blocks* (Fig. 2A, right)
346 and the blocks in which the target changed direction in fixation trials as it did in the
347 movement trials *congruent learning blocks* (Fig. 2A, middle). The learned response in the
348 fixation incongruent learning blocks could only result from the repetition of the eye
349 movement trials. Thus, if learning were driven solely by infrequent eye movement trials, we
350 would expect that the learned response would be similar on the congruent and incongruent
351 blocks. When tested on the infrequent (10%) eye movement trials the eye velocity in the
352 learned direction was lower in the incongruent than in the congruent learning blocks (Fig.
353 2B). Paired comparisons between nearby congruent and incongruent blocks that were
354 recorded the same day (but separated by at least one washout block - see Methods) indicated
355 that in most sessions, the learned response was higher in congruent blocks than in
356 incongruent blocks (Fig. 2C, signed rank test $p = 5.9 \times 10^{-6}$). These results indicate that fixation
357 trials play an important role in the development of the learned response.

358 This conclusion draws on the assumption that the contribution of the eye movement
359 trials to the learned response was identical in the fixation congruent and incongruent blocks.
360 To further confirm that the monkeys indeed learned from the congruent fixation trials, we
361 tested additional learning blocks. As in the fixation congruent trials, the target changed
362 direction in the fixation trials, but unlike the previous learning blocks we probed learning
363 using trials in which the target did not change direction (these trials were thus identical to the
364 eye movement trials in the washout blocks, see Methods) (Fig. 2D, left). The only signal that
365 could be used for learning in these blocks was the change in direction in the fixation trial. We
366 alternated blocks in which the fixation trials had opposite learned directions, i.e., left (Fig.
367 2D, middle) or right (Fig. 2D, right). Thus, this experimental design had the advantage that in
368 each learning block the monkeys never followed a target moving in the learned direction in
369 the eye movement trials and that on the fixation trials, the target always changed direction.

370 In the eye movement trials the average eye velocity deflected towards the learned
371 direction (Fig. 2E). Positive and negative values in this analysis indicate movement right and
372 left. Importantly, this deflection was not visually driven because the stimulus in eye
373 movement trials did not have any motion in the learned direction. Therefore, this deflection
374 could only have resulted from learning in fixation trials. To directly compare sessions, we
375 plotted the learned component in alternating blocks with the opposite learned directions. The
376 bias in the learned response towards the change in direction was manifested by the strong
377 tendency of the dots to plot beneath the equality line in Figure 2F (signed rank test,
378 $p = 7.7 \times 10^{-10}$). We found a slight difference between monkeys. In Monkey C the bias was
379 symmetric, i.e., in each learning block the eye moved towards the direction of the change in

380 target motion (positive and negative horizontal and vertical values, in open dots in Fig. 2F).
381 The movement of Monkey A was slightly biased towards positive values (corresponding to
382 motion to the right), as indicated by the positive values on the horizontal axis and close to 0
383 on the vertical axis shown by the open dots in Fig. 2F. Nevertheless, the comparison between
384 blocks indicated that in both monkeys the change in direction on the fixation trials biased the
385 learned eye velocity in the corresponding direction. Thus, the monkeys learned passively,
386 when the only signal for learning was the change in target direction on the fixation trials.

387 Control for movements in the fixation window

388 So far, we have shown that monkeys learn from fixation trials, suggesting that neither
389 the corrective movement nor the feedback on erroneous behavior was necessary for learning.
390 One possible confounding effect is that monkeys did not completely suppress behavior on the
391 fixation trials (solid traces in Fig. 3B and C). To control for this eventuality, we conducted
392 experiments to confirm that the behavioral responses on the fixation trials did not affect the
393 learned response.

394 In the learned direction on the fixation trials, we observed a very slight increase in the
395 velocity around the change in target direction in the congruent blocks compared to the
396 incongruent blocks (arrow marking the dashed gray and black traces in Fig 3C and the gray
397 trace in Fig. 3D). We aimed to mimic this behavioral difference to test whether it would
398 impact the learned response on motor trials. To mimic the visually driven eye movement in
399 the learned direction on congruent trials the monkeys were required on most trials (90%) to
400 track a moving target that changed direction slightly after 250 ms such that a small
401 component (0.5°/s) of the target velocity was added in the learned direction (Fig. 3A bottom
402 left). In the second block, which was designed to mimic behavior on incongruent trials, in
403 90% of the trials the target did not change direction (as in the eye movement trials in the
404 washout blocks, see Methods, Fig. 3A bottom right). As expected, the difference in eye
405 velocity in the learning direction between learning trials consisting of no angle and small
406 angle blocks (Fig. 3D, black) was indeed similar to the difference between fixations trials in
407 the congruent and incongruent blocks (Fig. 3D, gray). To keep the structures of the blocks as
408 similar as possible and to probe learning, in the remaining 10% of the trials, the target
409 changed direction as in the previous experiments (20°/s component in the learning direction,
410 Fig. 3A top).

411 If indeed the corrective behavior we observed on the fixation trials were sufficient to
412 drive learning we would expect to find a difference between the mimic blocks with and
413 without the small angle. However, we found that the difference between the learned response
414 eye velocity on blocks with small and no angle was not significant (Fig. 3E, Wilcoxon signed
415 rank test, $p=0.26$). Furthermore, the difference between the learned response in the congruent
416 versus incongruent blocks was larger than the difference between blocks with and without an
417 angle (rank-sum $p = 0.036$). Therefore, this control suggests that the slight corrective
418 movement we observed in the fixation trials did not drive learning.

419 Next, we focused on the increase in base velocity on fixation trials around the change
420 in direction in both the congruent and incongruent blocks (solid gray versus black traces in
421 Fig 3B, marked by an arrow). This movement might contribute to learning since the
422 discrepancy between the movement and the direction of target change could elicit an error
423 signal. However, if indeed this discrepancy between behavior and target motion drove
424 learning, we would expect that larger movements in the base direction would correlate with
425 more learning on the movement trials. However, in the congruent blocks, there was no

426 significant correlation between the base velocity averaged across the fixation trials and the
427 amplitude of the learned response on the subsequent test trial (Fig 3F, the multiple regression
428 analysis with monkeys and base velocity as predictors of learned velocity was significant for
429 monkeys, $p=3.02*10^{-13}$, but not for base velocity, $p=0.34$). Figure 3G and 3H show the
430 absence of correlation in time for Monkey A. We clustered the base velocity on the fixation
431 trials into three groups according to the magnitude of the base direction eye velocity on the
432 fixation trials (Fig. 3G). As expected from a non-correlated relationship, these clusters were
433 not preserved when we plotted the learned response on the fixation trials (Fig. 3H). These
434 result are consistent with a recent study using a motor learning paradigm which did not find a
435 correlation between movement speed in the base direction prior to change in the target
436 direction and learning on the next trial (Herzfeld et al. 2020). Thus, it is unlikely that
437 residual movement on the fixation trials within the fixation window was necessary for
438 learning.

439 Learning in fixation blocks is driven by the change in direction

440 We have shown that the monkeys were able to learn from fixation trials. We next
441 attempted to better understand which component in the fixation trials was necessary for
442 learning. In the eye movement trials, the crucial instructive signal for learning is the change
443 in target direction (Medina and Lisberger 2008; Yang and Lisberger 2014). Consequently, we
444 tested whether motion in the learned direction of the target is essential to develop the learned
445 response. Alternatively, information about the end point position of the target could be
446 sufficient to drive learning. To answer this question, we compared the learned response in
447 two learning blocks. The first block was identical to the fixation congruent block described
448 above (Fig. 4A, top and middle). In this context we termed this block the *motion block*. The
449 second block, termed the *position block* was similar to the previous block except that the
450 moving target vanished right before the addition of the upward velocity component, 250 ms
451 after motion onset. The target then reappeared at the end of the trial (650 ms after motion
452 onset) in the same position as in the motion trials (Fig. 4A, bottom). We found that the
453 learned response on the motion block was higher than on the position block (Fig. 4B). Single
454 session comparisons indicated that this difference was significant (Fig. 4C, Wilcoxon signed
455 rank test, $p=1.8*10^{-4}$), consistent across monkeys and observed in most sessions. Therefore,
456 instructing learning without target motion was less effective in driving passive learning. This
457 result highlights the important role of motion in the development of the learned response (see
458 discussion for possible interpretations).

459 Learned response in fixation blocks is modulated by expected reward

460 We have shown how basic sensorimotor parameters such as target motion and eye
461 movements impact learning. We next tested whether the task's broader context could also
462 influence learning from observation. Specifically, reward interacts with the visuomotor
463 processing of the pursuit system (Damasse et al. 2018; Joshua and Lisberger 2012; Lixenberg
464 and Joshua 2018). We therefore designed a task to test whether the learned response could be
465 modulated by reward information. The structure of the eye movement and fixation trials were
466 similar to those described in the first part of the experiment (Fig. 1A). Each block consisted
467 of 10% eye movement trials and 90% fixation trials. The fixation trials were equally divided
468 (45%) into congruent trials and incongruent trials. The key difference was that the reward
469 associated with each fixation trial was swapped between blocks. In the congruent-reward
470 blocks, a reward was only given after congruent trials (Fig. 5A, top) whereas in the
471 incongruent-reward blocks a reward was only given after incongruent trials (Fig. 5A,
472 bottom). The color of the target indicated whether the monkey would be rewarded at the end

473 of the trial (Fig. 5A). We tested learning in eye movement trials with a white target in which
474 the monkey always received a reward, to ensure that the reward in these trials did not affect
475 the expression of learning differently (Joshua and Lisberger 2012).

476 We found that reward modulated the amplitude of the learned response. The average
477 learned response on the eye movement trials was higher for the congruent-reward than for the
478 incongruent-reward blocks (Fig. 5B). Paired tests between interleaved blocks that were
479 separated by a washout block indicated this difference was significant ($p=6.1*10^{-5}$, signed
480 rank test) (Fig. 5C). These results corroborate the hypothesis that reward modulation affects
481 the acquisition of learning as was found in some paradigms of motor learning (Liu et al.
482 2019) but not in others (Joshua and Lisberger 2012). Here, we aimed to optimize the
483 conditions for finding an effect of reward on passive learning by making the experimental
484 conditions similar to experiments that have demonstrated that reward affects the acquisition
485 of motor learning (Liu et al. 2019). Therefore, we interleaved trials with different reward
486 outcomes and different effects on learning (incongruent/congruent). To compare the effects
487 of reward on motor and passive learning, a better characterization of the condition in which
488 reward drives the acquisition of motor learning is needed. This characterization is important
489 but beyond the scope of the current study. Note that prior to the experiment, the monkeys
490 were extensively trained to associate color with the reward (Larry et al. 2019; Lixenberg et al.
491 2020). Therefore, it is likely that the expected reward, rather than reward delivery, was the
492 critical reward signal modulating learning, perhaps through attention mechanisms.

493 *Very rapid learning is probably explained by the uniformity of the learning block.*

494 In the previous sections we considered learning blocks as a whole without addressing
495 the dynamics of learning. We calculated the learning curve in the fixation and motor blocks
496 by assessing the size of the learned response as a function of the number of trials (Fig. 6A).
497 In the fixation blocks we did not observe a progression in learning (Fig. 6A, dashed line),
498 indicating that most of the learning occurred prior to the first eye movement trial. In the
499 fixation blocks, the learned response on the first eye movement trial (which was followed
500 on average by 5 fixation trials) was not significantly different from the other eye movement
501 trials ($p=0.8$, rank-sum test). To test whether this quick learning was specific to the fixation
502 block, we analyzed the learning curve in the interleaved motor learning blocks. We found that
503 as in the fixation block, most of the learning occurred very rapidly (Fig. 6A, solid). To
504 quantify, we fit the learning curve to a double exponent (see Methods). We found that the
505 rapid learning ($\tau_1 = 4*10^{-2}$ trials) dominated the learning process in that it explained 68.46%
506 of the learning in the first 100 trials, suggesting that the absence of graduality in passive
507 learning was due to the high speed of learning.

508 The main goal of this study was to test whether monkeys can learn without tracking
509 the target. We therefore attempted to strictly control parameters such as the direction of
510 motion that a-priori seemed irrelevant. However, this choice might have led to the very fast
511 learning in motor blocks and our inability to detect changes in fixation blocks (Fig. 6A). To
512 test whether indeed restricting the direction led to the fast learning, and to test for dynamics
513 in the passive learning we conducted an experiment in which we enriched the context by
514 varying the base ($0^\circ, 90^\circ, 180^\circ$ or 270°) and learned (clockwise and counter clockwise)
515 directions of the fixation congruent and motor blocks (on two other monkeys). The learning
516 curve in this richer context increased gradually in both the fixation and motor learning blocks
517 (Fig. 6B and C). In the motor blocks rapid learning dropped to 56% of the total learning and
518 was slower than in the homogeneous context ($\tau_1 = 1.2$ trials). Thus, the richness of the

519 direction influences the learning dynamics as do other task parameters such as the time
520 between consecutive learning trials or different trials interleaved between learning trials.

521

522 **Discussion**

523 *Passive motor learning*

524 It is well-established that monkeys learn to predict a change in target direction when
525 actively tracking the target (Medina et al. 2005). Here, we found that a passive observation of
526 the change in target direction without tracking is sufficient to elicit a learned response. Thus,
527 an association between motor output and sensory feedback is not necessary to elicit an
528 adaptive response. Other studies on adaptation paradigms have highlighted the importance of
529 sensory feedback on movement in learning (Held and Freedr 1963; Mazzone and Krakauer
530 2006; Mostafa et al. 2019). All these paradigms have reported a discrepancy between the
531 predicted and observed sensory outcomes of motor commands (Shadmehr et al. 2010). For
532 example, application of a force field is known to change the observed sensory outcomes of a
533 given motor command. The smooth pursuit paradigm presented here differs from these
534 paradigms in that the perturbation (the change in direction of the moving target) can be
535 perceived without movement so that learning does not depend on the predicted sensory
536 outcomes of a motor command. This difference may explain why the pursuit system could be
537 more amenable to passive motor learning.
538

539 Nevertheless, it remains unclear which signals drive passive learning. There are at
540 least two possible mechanisms governing the ways in which velocity signals in fixation trials
541 could drive learning. The first is that velocity is an arbitrary cue associated with the direction
542 of movement on eye movement trials. This type of cue might be used as a signal for
543 switching movement in the subsequent eye movement trial according to the direction of the
544 moving target in the fixation trials. The second possible mechanism is that learning acts
545 specifically on the velocity signals. The position experiment (Fig. 4) lends more weight to the
546 latter alternative since it showed that another relevant cue, the position of the target at the end
547 of the movement trials, drove less learning, thus suggesting that passive learning is not
548 exclusively underpinned by switching the movement between blocks. Additional evidence for
549 the importance of velocity signals beyond arbitrary rules comes from pursuit motor learning
550 in which target motion direction rather than abstract rules such as alternation of the learned
551 direction drive motor learning (Yang and Lisberger 2010). Thus, it is probable that in the
552 pursuit learning, velocity signals play a unique role. However, we cannot completely refute
553 the possibility that the velocity, as a very salient signal, was easier for the monkeys to
554 interpret as a cue.
555

556 Overall, passive (as well as motor) learning in smooth pursuit in monkeys is probably
557 mostly implemented through the sensorimotor representation of the target motion rather than
558 an abstract representation. The smooth pursuit eye movement system has been widely used as
559 a model system for studying sensorimotor transformation and motor learning at the
560 implementation level of neurons and networks (Joshua and Lisberger 2015; Lisberger 2010).
561 The paradigm we developed here can be harnessed to provide testable hypotheses on where
562 and how the brain implements passive learning. Another advantage of this paradigm stems
563 from the temporal gap between the sensory inputs on the fixation trials and their effect on
564 later motor trials. Thus, this paradigm provides an easy way to dissociate between the
565 processing of visual motion and the generation of pursuit motor commands for the upcoming
566 movement.
567

568 Possible Neural implementation in the cerebellum and frontal cortex

569 The cerebellar flocculus plays an important role in the development of a predictive
570 response to an instructive change in target direction during active motor learning (Medina
571 and Lisberger 2008). According to the classic cerebellar model, sensory errors resulting from
572 inaccurate movement drive climbing fiber input (Albus 1971; Gilbert and Thach 1977; Ito
573 1972). The climbing fiber input, paired with input to the Purkinje cell, results in an
574 associative reduction in synaptic strength (Ito et al. 1982; Suvrathan et al. 2016). This
575 reduction is thought to underlie the subsequent improvement in behavior.

576 Tracking is not necessary for climbing fiber activation, as a task-irrelevant
577 background motion was shown to have a substantial effect on the climbing fiber response
578 (Guo et al. 2014). Similarly, motion of the background in fixation trials (i.e. the moving
579 target), may drive climbing fiber input as well. The error signal in this framework might be
580 the predicted motion of the target relative to the actual moving target trajectory. In addition,
581 to elicit behavioral learning, climbing fiber activation must be coupled with the appropriate
582 parallel fiber input. It is possible that the appropriate parallel fibers are also activated during
583 fixation trials since some of the activity of the Purkinje cell is driven by sensory responses
584 (Krauzlis and Lisberger 1991) or might reflect a motor command that is cancelled
585 downstream. According to this hypothesis, the same cerebellar mechanisms would drive
586 active and passive learning. At the neuronal level, it predicts that all the hallmarks of
587 cerebellar learning will be observed during passive learning. For example, in fixation trials
588 climbing fiber inputs will be modulated during the target change of direction. Furthermore,
589 the Purkinje cell simple spikes are likely to be tightly related to the climbing fiber input on a
590 trial-by-trial basis (Herzfeld et al. 2018; Medina and Lisberger 2008; Suvrathan et al. 2016).
591 The presence of a climbing fiber response after the change in direction on one trial should be
592 associated with a change in the simple-spike firing rate on the subsequent fixation or eye
593 movement trial.

594 Passive learning could be implemented in the FEF. Visual, motor and temporal
595 signals converge in the FEF (Bruce and Goldberg 1985; Macavoy et al. 1991; Schafer and
596 Moore 2011; Schall et al. 1995; Schoppik et al. 2008; Sommer and Wurtz 2006). During
597 pursuit learning neurons that are temporally tuned to the time of target change in direction are
598 those that undergo the largest learning modulation (Li et al. 2011). If time tuning is preserved
599 during fixation trials it might underlie passive learning. For example, during fixation, neurons
600 that are tuned to the direction and time of the change in the target direction would respond the
601 most vigorously. Any inputs to these cells from other cells that are tuned to the base direction
602 prior to the time of change in direction would be potentiated through spike-timing dependent
603 plasticity. This plasticity process should result in an increase in activity of neurons tuned to
604 the learning direction even before the change in direction in fixation and motor trials.

605 Another possible learning mechanism may occur upstream from the FEF. The SEF is
606 a good candidate for learning the association between the movement in the base direction and
607 the addition of a component in a learned direction (Chen and Wise 1995; Fukushima et al.
608 2004). The change in SEF activity would elicit a learned response through the reciprocal
609 connections between SEF and FEF (Huerta et al. 1987). Thus, there are several plausible sites
610 in which observed information could be used to drive learning. Future work probing and
611 manipulating these networks, could use the paradigm we describe here to study the
612 implementation of motor adaptation learning in the absence of behavioral errors.

613 Quantification of learning from fixation trials

614 The learned response shown in fixation blocks (Fig. 1) can be divided into two
615 components: the passive learning elicited by fixation trials and the motor learning that
616 resulted from the test trials. The trials assessing learning are also involved in the learning
617 process; therefore, we cannot directly measure the learning elicited exclusively by passive

618 learning. Indirect measures suggest that most learning in fixation blocks is due to passive
619 learning. The learned response in the first test trial, which was preceded only by fixation
620 trials, was similar to the learned response late in learning (Fig. 6A) and the learned response
621 in the incongruent blocks was small (Fig. 2B).

622 Although we cannot completely control for the magnitude of learning from eye
623 movement trials, we can bound the amplitude of the learned response elicited by the fixation
624 trials. The learned response in the fixation blocks constitutes an upper bound for the
625 amplitude of the learned response elicited by fixation trials because it contains both passive
626 learning and a small component of motor learning. The learned response in the experiment in
627 which the target only changed direction on fixation trials (Fig. 2E) constitutes a lower bound
628 for learning from fixation trials. In these blocks learning was assessed using non-adaptive
629 probe trials that reduced the learning elicited by fixation trials. We quantified these bounds
630 by calculating the ratio of the learned response in the motor block to the learned response in
631 the corresponding block. We estimated that passive learning in the current paradigm lay
632 within a range of 18% and 48% (see Methods) of the total motor learning (learning in eye
633 movement blocks; e.g., Fig. 1C). This estimation may not be the theoretical limit since other
634 non-motor factors could account for the difference between passive and motor learning. For
635 example, attention or the exact location of the stimulus on the retina at the time of the change
636 in direction could have varied across the eye movement and fixation trials. Further research
637 should consider the interaction between learning mechanisms elicited by motor and non-
638 motor signals in the presence of movement. Passive learning might be elicited concurrently
639 with mechanisms driven by motor signals or alternatively be elicited exclusively in the
640 absence of a motor signal.

641 Overall, we showed that the passive observation of target motion can drive behavior
642 characterized as motor adaptation learning. We conducted controls and explored the
643 conditions in which passive learning is expressed. The pursuit system provides a unique
644 model system for studying passive learning since it can be explored at the implementation
645 level in monkeys. We suggest possible mechanisms based on the known properties of the
646 smooth pursuit system. These hypotheses can serve as the basis for further investigations of
647 passive motor learning in the pursuit and other systems.
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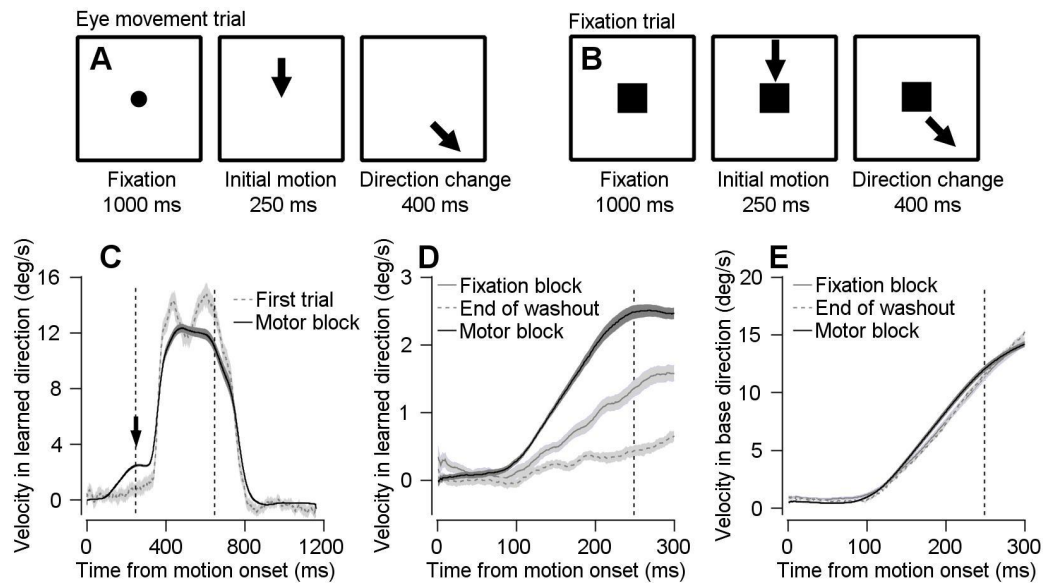
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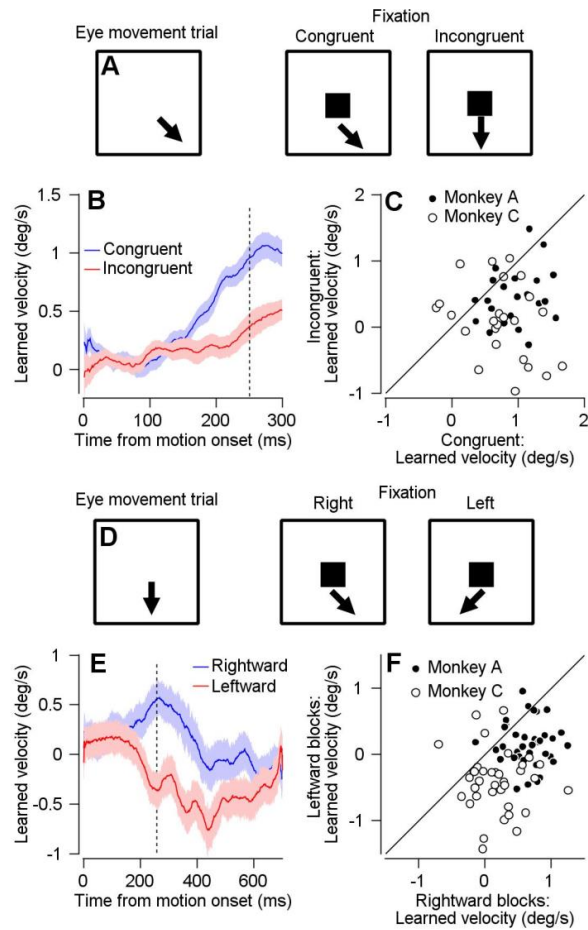
751 **Figure 1. Trial schematics and behavior in motor and fixation blocks.** **A, B:** Schematics
 752 of the eye movement (A) and fixation (B) trials. Arrows show the direction of target motion,
 753 circle represents the target prior to motion onset and squares represent the fixation target. **C:**
 754 Average eye movement in the learned direction on the first trial of learning (dashed gray
 755 trace) and post-learning trials (50th to 100th trial) averaged across all motor blocks (black). **D,**
 756 **E:** Average eye movement in the learned (**D**) and base (**E**) directions at the end of washout
 757 blocks (25 last eye movement trials, dashed gray) and after learning on motor blocks (50th to
 758 100th trial averaged across all motor blocks, solid black) and fixation blocks (5th to 10th
 759 eye movement trials averaged across all congruent fixation blocks, solid gray). In all traces,
 760 shadowing represents SEM. Vertical dashed lines show the time of the change of direction
 761 (250 ms) and end of target motion (650 ms).

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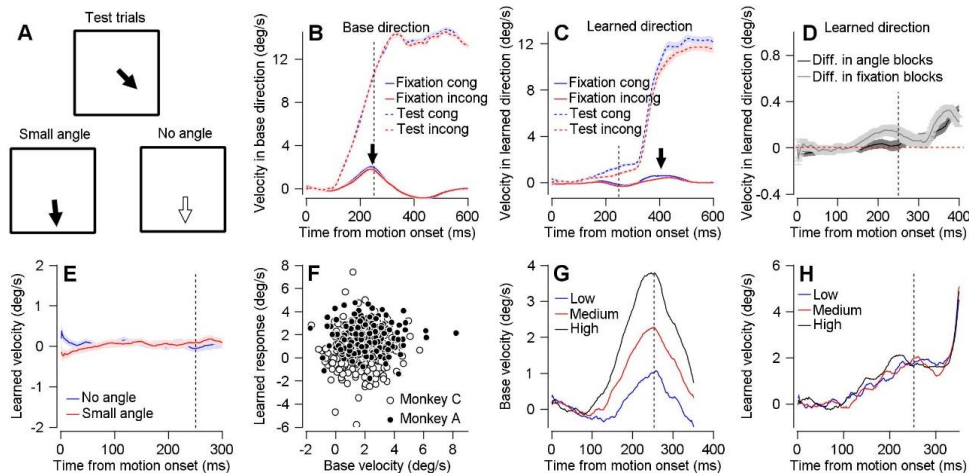
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Figure 2: Learning from observation is not driven solely by infrequent eye movement trials. **A:** Schematics represent the direction change epoch in the different experimental conditions. Left: eye movement trials with change in direction, middle: congruent trial-fixation trial with directional change, Right: incongruent trial- fixation trial without directional change. **B:** Average learned eye velocity as a function of time from motion onset for eye movement trials averaged across all congruent (blue) and incongruent (red) blocks. **C:** Learned response on incongruent (vertical) versus congruent (horizontal) blocks. Filled and open symbols show data from monkeys A and C. Solid line indicates unity. **D:** Schematics represent the target motion in the different experimental conditions. Left: eye movement trials without a change in direction, Middle: fixation trials in which rightward is the learned direction, Right: fixation trial in which leftward is the learned direction. **E:** Average learned eye velocity in eye movement trials averaged across all learning blocks as a function of time from motion onset in blocks in which the moving target moved rightward (blue) or leftward (red). **F:** Learned response in adjacent blocks in which on fixation trials the target moved rightward (horizontal) or leftward (vertical). Filled and open symbols show data from

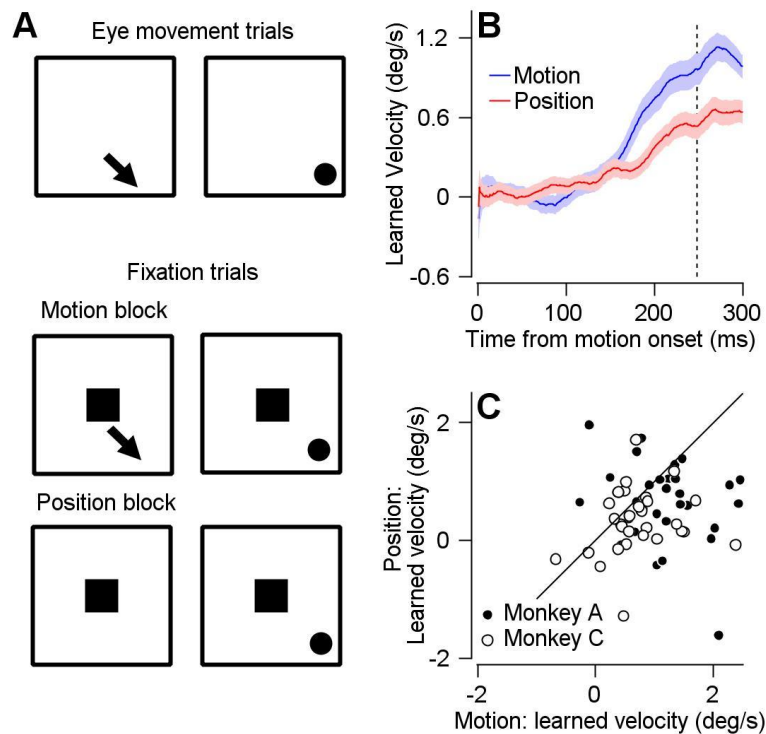
787 monkeys A and C. Solid line indicates unity. In all traces, shadowing represents the SEM.
 788 Vertical dashed line shows the time of the change in direction of the moving target.
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 791 **Figure 3: Learning is not driven by residual movement on fixation trials.** **A:** Schematics
 792 showing the direction of motion change on trials with large (top), small (bottom left) and no
 793 change (bottom right) in target direction. **B, C:** Eye velocity in base (**B**) and learned (**C**)
 794 direction as a function of time from motion onset on fixation (solid trace) and test (dashed
 795 trace) trials. Blue and red traces show the velocity averaged across congruent and incongruent
 796 fixation blocks. **D:** Difference in learned eye velocity between fixation trials from congruent
 797 and incongruent blocks (gray) and difference between trials with small and no angle in the
 798 corresponding blocks (black). Dashed red line indicates null velocity **E:** Average learned eye
 799 velocity as a function of time from motion onset in test trials in blocks without change in
 800 direction (blue) and with a small change in direction (red). **F:** Base velocity on fixation trials,
 801 average from 200 ms up to 300 ms after motion onset versus learned response in subsequent
 802 test trials in fixation congruent blocks. Filled and open symbols show data from monkeys A
 803 and C. **G, H:** Base velocity on fixation trials (**G**) and learned velocity on eye movement trials
 804 (**H**) in fixation congruent blocks as a function of time from motion onset for group of fixation
 805 trials with low, medium and high base velocities (blue, red and black traces). In all traces,
 806 shadowing represents the SEM. Vertical dashed line shows the time of the change in
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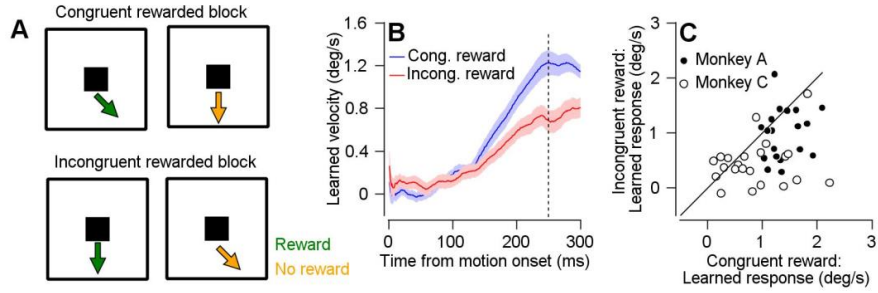


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 811 **Figure 4: Learning on fixation blocks is driven by change in direction.** **A:** Schematics
 812 represent the target motion and position at the beginning and end of direction change epochs.
 813 Arrow represents the direction of motion; squares represent the fixation target and dots
 814 represent the location of the moving target at the end of the trial. Top: eye movement trials
 815 with change in direction. Middle: Fixation trials in blocks with target motion. Bottom:
 816 Fixation trials in blocks without target motion - the moving target vanished with the change
 817 in direction and reappeared at the end of the epoch. **B:** Average learned eye velocity as a
 818 function of time from motion onset in learned direction in eye movement trials averaged
 819 across all motion (blue) and position (red) blocks. **C:** Learned response in eye movement
 820 trials on motion (horizontal) versus position (vertical) blocks. Solid line indicates unity.
 821 Filled and open symbols show data from monkeys A and C. In all traces, shadowing
 822 represents the SEM. Vertical dashed line shows the time of the change in direction of the
 823 moving target

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829 **Figure 5: Learning on fixation blocks is modulated by expected reward.** **A:** Top: fixation

830 trials in congruent rewarded blocks- Left: congruent rewarded trials, Right: incongruent

831 unrewarded trials. Bottom: fixation trials in incongruent rewarded blocks- Left: incongruent

832 rewarded trials, Right: congruent unrewarded trials. Colors correspond to the color of the

833 target used for monkey C. For monkey A blue and pink signaled reward and omission of

834 reward. **B:** Learned eye velocity as a function of time from motion onset averaged across all835 eye movement trials in congruent rewarded (blue) and incongruent rewarded (red) blocks. **C:**

836 Learned response in congruent rewarded (horizontal) versus incongruent rewarded (vertical)

837 blocks. Solid line indicates unity. One outlier that had values of (0.52; -1.53) is not shown.

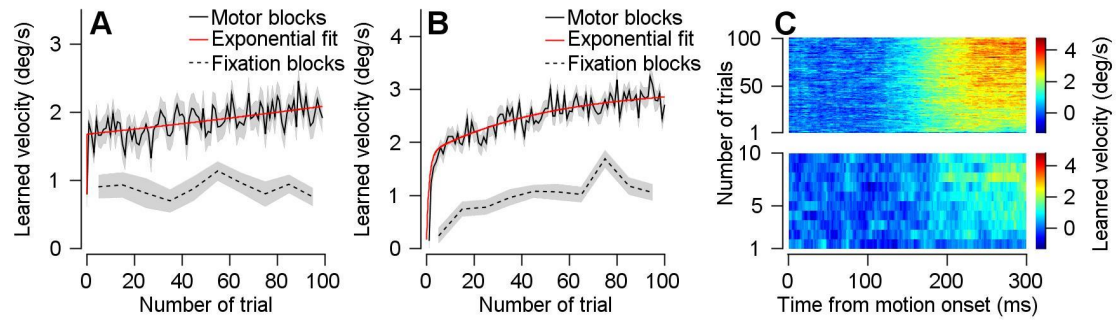
838 Filled and open symbols show data from monkeys A and C. In all traces, shadowing

839 represents the SEM. Vertical dashed line shows the time of the change in direction of the

moving target

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841



842
 843 **Figure 6: Learning dynamics in motor and fixation congruent blocks.** **A, B:** Learning
 844 curve for motor (solid) and congruent fixation blocks (dashed) with single (**A**) or multiple (**B**)
 845 base and learned directions. Exponential fit of the motor learning curve is shown in red. In all
 846 traces, shadowing represents the SEM. **C:** Learned velocity in eye movement trials averaged
 847 across all motor (up) and fixation blocks (bottom). Colors represent learned velocity, and
 848 each horizontal line of the image shows eye velocity as a function of time for a single trial.
 849 The trials in a learning block progress from the bottom to the top of the image. The left plot
 850 shows data from monkeys A and C; the middle and right from monkeys E and F.
 851