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4 Role of motor execution in the ocular tracking of
5 self-generated movements

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23 Running Head: Role of motor execution in ocular tracking of self movements

24 Keywords: Anticipatory smooth pursuit;

25 Ocular tracking of self-motion;

26 Congruency effect;

27 Eye-hand coordination;

28 **Abstract**

29 When human observers track the movements of their own hand with their gaze,
30 the eyes can start moving before the finger (i.e., anticipatory smooth pursuit). The
31 signals driving anticipation could come from motor commands during finger motor
32 execution or from motor intention and decision processes associated with
33 self-initiated movements. For the present study, we built a mechanical device that
34 could move a visual target either in the same direction as the participants' hand or in
35 the opposite direction. Gaze pursuit of the target showed stronger anticipation if it
36 moved in the same direction as the hand, compared to that in the opposite direction, as
37 evidenced by decreased pursuit latency, increased lead of the eye to target in positions,
38 decreased saccade rate, and decreased delay at the movement reversal. Some degree
39 of anticipation occurred for incongruent pursuit, indicating that there is a role for
40 higher-level movement prediction in pursuit anticipation. The fact that anticipation
41 was larger when target and finger moved in the same direction provides evidence for a
42 direct coupling between finger and eye motor commands.

43

44 **New & Noteworthy**

45 Humans constantly coordinate eye and hand movements. Here we asked
46 observers to track their own finger movements, and found that, in every aspect of
47 tracking measurements, the tracking performance was better when the eye and hand
48 was moving in a congruent direction. As we made sure that top-down predictability
49 was identical, our results showed that directly mapped motor commands plays a role
50 in eye hand coordination.

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58 **Introduction**

59 We constantly coordinate our eye and hands when we interact with the world.
60 One example of such coordination is when our gaze follows our moving hand. Studies
61 have shown that the ocular tracking of self-generated movements is better than the
62 tracking of external movements. The benefits include reduced pursuit latency
63 (Gauthier and Hofferer 1976; Scarchilli and Vercher 1999; Ross and Santos, 2014),
64 decreased number of saccades (Mather and Lackner 1980; Steinbach and Held 1968;
65 Steinbach 1969), and reduced delays at reversals (Mather and Lackner 1980;
66 Steinbach 1969; Vercher et al. 1995). Two models have been proposed to explain
67 these effects: the common controller model (Bock, 1987) and the mutual coordination
68 model (Lazzari et al. 1997; Scarchilli and Vercher, 1999). The common controller
69 model suggests that a common control signal is fed to both the pursuit system and the
70 hand motor system for coordinated movements, without a direct link between two
71 systems. Direct evidence for the common controller model comes from the
72 observation that executing smooth pursuit eye movements modulates the excitability
73 of the hand motor cortex, as evidenced by motor evoked potentials measured after
74 applying transcranial magnetic stimulation (TMS) to the primary motor cortex
75 (Hiraoka et al. 2014; Maioli et al. 2007). The mutual coordination model does not
76 include a common control stage and instead assumes that the two systems exchange
77 information constantly and directly. For example, Scarchilli and Vercher (1999)
78 showed that the somatomotor and oculomotor systems independently adapt to
79 predictable mechanical perturbations applied to the hand, yielding optimal
80 coordination. Hwang, Hauschild, Wilke and Andersen (2014) investigated the role of
81 the parietal reach region, an area responsible for hand reach movement in eye-hand
82 coordination. They found that inactivation of the parietal reach region impairs
83 coordination, revealing a direct interaction between hand movement system and eye
84 movement system. These results thus support the mutual coordination model.

85 The two models are of course not mutually exclusive, since a common control
86 signal for eye and hand movements could be fine-tuned by additional coordination
87 signals. It is plausible that a common control signal resulting from motor decisions in

88 the motor planning stage is followed by interactive coordination signals from the
89 efference copy of the motor command in the motor execution stage. A preliminary
90 report (Kowler et al., 2015) suggested a dominant role of the decision signals for
91 eye-hand coordination, by showing that pursuit could still be initiated with near-zero
92 latency even when the efference copy signal was disrupted by mirroring the direction
93 of the eye and the direction of the hand. Indeed, a recent primate study showed that
94 neural signals in the lateral intraparietal area (LIP) in the motor planning stage
95 predicted eye movements made in coordination with hand, but not eye movements
96 executed alone. These studies implied a crucial role of decision signals from hand
97 motor preparation in the control of eye movement. It is unknown, however, whether
98 coordination signals from on-going motor execution also plays a role in coupling the
99 eye and hand movement.

100 In the present study we aimed to separate the contribution of low-level signals
101 coming from motor execution from the contribution of high-level decision-based
102 signals. To this aim, we built a mechanical device that could move a visual target
103 either in the same direction as the participants' hand or in the opposite direction. In
104 each block of trials, the finger and eye movement directions were either congruent or
105 incongruent, and observers repeatedly moved their finger to the same direction,
106 ensuring complete predictability of the target motion in either case. In the incongruent
107 blocks low-level signals anchored to the finger motor commands would however be
108 incompatible with the oculomotor task. Our results show improved tracking
109 performance in the congruent blocks compared to incongruent blocks, suggesting that
110 directly mapped low-level motor commands plays a role in the oculomotor
111 anticipation of finger movements.

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118 **Method**

119 *Participants*

120 Twelve observers (7 females, average age = 26.6, from 20 to 36) participated in
121 the experiment. They had normal or corrected-to-normal vision, and were all
122 right-handed. They signed written informed consent forms in agreement with the
123 Declaration of Helsinki and approved by the local ethics committee.

124

125 *Procedure*

126 The experiment took place in a lit room. Participants used their right index finger
127 to control the device. Participants initiated a trial by pressing the space bar on the
128 keyboard with their left hand. To correct gaze drift due to, e.g., minor eye movements,
129 we measured the gaze positions for 400 ms following the bar pressing and subtracted
130 the fixation error. After a 100-ms delay, an audio cue indicated the start of the trial.
131 Participants then started to move their right finger to either the left or the right
132 direction, and to move back to center. The direction of motion was constant in a given
133 block of trials and alternated between blocks. Participants were instructed to make a
134 smooth movement, in particular they were asked to turn smoothly without stopping
135 the movement at the turning point. They were told not to move too far so as not to
136 reach the limit of the range enabled by the device (17 cm, i.e., 32.5 deg, on either
137 side). There were no further constraints on the amplitude or speed of their movement.
138 Meanwhile, their gaze should keep following the tracking target, which could move
139 either congruently with the finger, or incongruently across different blocks. Within a
140 certain block, however, both the hand direction and gaze direction remained constant;
141 participants thus were fully aware of the mapping between the tracking target and the
142 hand. Before each block, participants were explained the mapping of this block and
143 were encouraged to try out before the block starts. The sequences of 4 blocks
144 (left/right hand moving direction, congruent/incongruent gaze-hand mapping) were
145 counterbalanced across participants. Participants underwent 320 trials in total (80 in
146 each condition), except for participant #1 who completed 480 trials (120 in each
147 condition). Participants took a short break and re-calibrated the eye tracker every 40

148 trials.

149

150 *Experimental Device*

151 We built a device that was controlled by the participants' finger (Fig 1). When
152 participants moved the finger horizontally, a marker for the Zebris motion tracker
153 system (Zebris Medical, Isny im Allgäu, Germany) on top of the device moved either
154 in the same direction as the finger, or in the opposite direction. The marker served as
155 the pursuit target, which was white in color and had a radius of 0.9 deg in a viewing
156 distance of 30 cm. The Zebris marker was chosen as the pursuit target mostly for
157 convenience. On one side it would have been difficult to occlude it from the viewer's
158 vantage point while leaving it in the field of view of the Zebris sensor. On the other
159 side, its shape resembles the commonly used bull's eye fixation targets. A belt inside
160 the device transmits the finger position to the target. An electric magnet under the
161 control of our experiment program engaged the target on different sides of the belt, so
162 that it moved either in the same direction as the finger or in the opposite direction.
163 This ensured that the mechanical resistance of the device was equated in both
164 configurations. Only the tracking target was visible to participants. All mobile parts of
165 the device and the hand were occluded to the observer.

166 [-----insert Fig 1 here-----]

167

168 *Target movement and eye movement recordings and analyses*

169 Movements of the pursuit target, which was directly connected to the finger, were
170 tracked at 100 Hz with a Zebris motion capture system (Zebris Medical, Isny im
171 Allgäu, Germany). The Zebris marker was attached to the experimental device and
172 served as pursuit target. Eye movements from the right eye were recorded at 1000 Hz
173 using an Eyelink 1000 table-mounted eye tracker (SR Research, Mississauga, ON,
174 Canada). We had to place the eye tracker behind the experimental device, as
175 participants need to interact with the device. Positioning the eye tracker above the
176 gaze, however, produced relatively noisy data. A chin rest was used to limit the head

177 movements. The distance from the eye to the pursuit target was 30 cm.

178 External motion tracking systems inevitably add some delay between the real
179 movement and the digital recording of the measurement. We estimated the delay of
180 the Zebris system by simultaneously recording the same movement with Zebris
181 system as well as a potentiometer with a rotating sensor (Vishay Spectrol 534, Vishay
182 Intertechnology, Inc., PA, USA). We then used the movement onset detection method
183 (Schütz et al. , 2007) described below to get the movement onset from both the
184 distance data of Zebris system as well as the voltage data of the potentiometer. With
185 100 measures, we estimated the delay as 9.0 ms (SD = 6.5 ms).

186 We manually checked the eye position and finger position traces for all trials.
187 Trials with artifacts, e.g. participants' failure to make the correct movement or eye
188 tracker data loss, were rejected (6.6%). We did not discard trials where saccades
189 occurred during fixation, as we expected eye movements to be executed anticipatorily.
190 We used the regression-based method described in Schütz et al. (2007) to compute the
191 finger and eye movement onset in individual trials. Position signals were low-pass
192 filtered below 30 Hz. Velocity signals, which were calculated by differentiating the
193 position data, were low-passed filtered below 20 Hz. We fitted regression lines with
194 80-ms length to the velocity trace, and discarded regression lines with $R^2 < 0.7$ or with
195 a slope below $10 \text{ }^\circ/\text{s}^2$ or above $200 \text{ }^\circ/\text{s}^2$. We then selected the regression line with the
196 highest R^2 value. The time corresponding to 0 velocity was defined as the movement
197 onset. Individual trials were visually inspected. When the estimated onset clearly
198 missed the initial build-up stage of the velocity trace (e.g., it was located at the
199 fixation stage or during on-going movement), we manually restricted the time window
200 to a range near the velocity build-up stage and repeated the above procedure to detect
201 the movement onset (we did this in 3.0% of trials for the finger onset detection; 28.7%
202 for the eye onset detection). Results did not change whether these trials were included
203 or not.

204 Saccades were detected using the EyeLink default algorithm, which uses a
205 velocity threshold of $30 \text{ }^\circ/\text{s}$ and an acceleration threshold of $8000 \text{ }^\circ/\text{s}^2$. The eye
206 movement latency was defined as the eye movement onset time relative to the finger

207 movement onset time (i.e., the visual target's movement onset time). Negative
208 latencies thus indicate anticipatory eye movements. Bimodality was statistically tested
209 with Hartigan's dip-test (Hartigan 1985; used in, e.g., Mergenthaler and Engbert,
210 2010), with a bootstrap sample size of 5000. Two tailed one sample t-test and
211 paired-samples t-test were used in all analyses. In the result, we reported
212 inter-individual standard deviation (SD) values together with the mean.

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229 **Results**

230 On average, the finger movement length before turning back was 14.6 deg (7.7 cm,
231 from 9.1 to 21.6 deg across participants, SD = 4.0 deg). The time of the turning point
232 was 737 ms on average, which varied between 296 and 1844 ms across different trials
233 and different participants. The average speed on the forward leg of the movement was
234 22.1 deg/s (between 14.1 and 36.8 deg/s across participants, SD = 8.6 deg/s). In Fig 2,
235 we plotted the average position and average velocity profile for one example observer.
236 We did not observe any significant difference between hand movements to the left and
237 to the right thus we grouped them together in all analyses.

238

239 [-----insert Fig 2 here-----]

240

241 We first explored how well participants coordinated their finger and eye
242 movements. For each participant, we correlated their finger onset time (relative to the
243 audio cue) and the eye onset time in both the congruent condition and the incongruent
244 condition. The correlation coefficient was on average 0.69 (SD = 0.17, from 0.36 to
245 0.91 across participants, all $P < .001$) in congruent pursuit and 0.75 (SD = 0.15, from
246 0.55 to 0.96, all $P < .001$) in incongruent pursuit. Across participants, finger onset
247 time highly correlated with eye onset time, both in the congruent condition ($r = 0.94$,
248 $P < .001$, Fig 3A) as well as in the incongruent condition ($r = 0.97$, $P < .001$, Fig 3B).
249 Moreover, the variability of finger onset time correlated with the variability of eye
250 onset time in the congruent condition ($r = 0.79$, $P = .002$) and the incongruent
251 condition ($r = 0.91$, $P < .001$). Furthermore, we computed the peak velocities of finger
252 movement and eye movement in the outgoing leg of the movement in individual trials.
253 Within each participant, the peak velocity correlation between finger and eye was on
254 average 0.42 (SD = 0.19) in congruent pursuit, and 0.25 (SD = 0.14) in incongruent
255 pursuit. The correlations were significant ($P < .05$) except in the case of one
256 participant in the congruent condition, and except for two participants in the
257 incongruent condition. Across participants, the peak velocities of eye and finger were

258 high correlated in both the congruent condition ($r = 0.94$, $P < .001$) and the
259 incongruent condition ($r = 0.76$, $P = .004$). These results demonstrated that
260 participants coordinated the finger and eye movements in both the congruent and
261 incongruent conditions

262 *Eye latency was reduced in congruent pursuit.* We compared the onset times
263 relative to the audio cue across conditions. Repeated-measures 2 (congruent vs.
264 incongruent) by 2 (finger vs. eye) ANOVAs over onset time revealed a significantly
265 earlier eye onset (mean \pm SD, 341.7 ± 71.7 ms) than finger onset (360.9 ± 69.3 ms),
266 $F(1, 11) = 10.1$, $P = .009$, and a significant interaction, $F(1, 11) = 15.0$, $P = .003$. The
267 main effect of congruency was not significant, $F(1, 11) = 3.6$, $P = .085$. Subsequently,
268 we first separately analyzed the congruent and incongruent condition. In congruent
269 condition, the eye onset (315.3 ± 68.6 ms) was significantly earlier than the finger
270 onset (347.7 ± 67.6 ms), $t(11) = -4.7$, $p = .001$. In incongruent condition, the eye onset
271 (368.0 ± 93.9 ms) and finger onset (374.1 ± 96.3 ms) did not differ, $t(11) = -0.9$, p
272 $= .40$. We then separately looked at the two modalities. The finger onset did not differ
273 between congruent (347.7 ± 67.6 ms) and incongruent condition (374.1 ± 96.3 ms),
274 $t(11) = -1.38$, $P = .19$; while the eye onset was earlier in congruent (315.3 ± 68.6 ms)
275 than incongruent condition (368.0 ± 93.9 ms), $t(11) = -2.3$, $P = .043$.

276 We calculated eye latencies as defined by eye onset time relative to finger onset
277 time (Fig 3C and 3D). Eye latencies were smaller in congruent condition (mean \pm SD,
278 -32.4 ± 23.9 ms) than that in incongruent condition (-6.1 ± 24.2 ms), $t(11) = -3.87$, P
279 $= .003$. Note that absolute latency should be treated with caution, as we may
280 underestimate it due to the delay in Zebris motion tracker system (9.0 ms based on our
281 estimate, see Method section). To quantify the variability of eye latencies, we
282 computed the standard deviations in each condition and for each participant, and
283 found no significant difference between the congruent condition (75.4 ± 24.6 ms) and
284 the incongruent condition (78.7 ± 35.0 ms), $t(11) = -0.39$, $P = .70$. We tested the
285 bimodality of eye latency distributions (Fig 3D for one example participant's latency
286 distributions). To avoid artifacts from averaging across participants, we ran the
287 analysis for each condition of individual participants. We did not find any significant

288 deviation from unimodality for any observer in both the congruent condition (all
289 $P > .52$) and the incongruent condition (all $P > .50$).

290

291 [-----insert Fig 3 here-----]

292

293 *Congruency effect does not quickly disappear with adaptation.* A previous study
294 suggest that the incongruency cost may be limited to the first few trials (Vercher,
295 Quaccia and Gauthier, 1995). We thus examined the eye latencies in the first 10 trials
296 (1-10), the following 70 trials (11-80), the following 40 trials (81-120) and the last 40
297 trials (121-160), separately in congruent and incongruent condition (Fig 4). A 2
298 (congruent vs. incongruent) by 4 (trial order) ANOVA revealed a main effect of
299 congruency, $F(1,11) = 17.2$, $P = .002$. The main effect of trial order was approaching
300 significance, $F(3, 33) = 2.26$, $P = .099$, while the interaction was not significant, $F(3,$
301 $33) = 1.12$, $P = .35$. Although some degree of adaptation might take place, participants
302 were not able to fully adapt to the incongruent condition, as evidenced by the fact that,
303 in the last 40 trials, we still observed a reduced eye latency in congruent pursuit (mean
304 = -35.2 ms, SD = 30.3 ms) than incongruent pursuit (mean = -18.8 ms, SD = 18.7 ms),
305 $t(11) = -2.69$, $P = .021$.

306

307 [-----insert Fig 4 here-----]

308

309 *Position lead was larger in congruent pursuit.* Not only did the eye start to move
310 before the finger, the eye also led the finger in position during on-going pursuit. We
311 measured how much the eye led the finger in both congruent pursuit and incongruent
312 pursuit (Fig 5A). In the [0 400] ms window, the lead was on average 0.29 deg in
313 congruent pursuit (SD = 0.41 deg; larger than 0, $t(11) = 2.49$, $P = .03$) and 0.03 deg in
314 incongruent pursuit (SD = 0.55 deg; not different from 0, $t(11) = 0.21$, $P = .84$). The
315 lead was significantly larger in congruent pursuit than that in incongruent pursuit, $t(11)$
316 = 2.96, $P = .013$. We measured the temporal lead by calculating the asynchrony

317 between the time the eye and the finger reached a given position (from 0.5 to 5 deg, in
318 0.02 deg bins, Fig 5B). In the [0.5 2] deg window, the temporal lead was 22.5 ms on
319 average in congruent pursuit (SD = 12.1 ms; larger than 0, $t(11) = 6.44$, $P < .001$) and
320 8.7 ms in incongruent pursuit (SD = 17.5 ms; not different from 0, $t(11) = 1.73$, P
321 = .11). The lead was larger in congruent pursuit than that in incongruent pursuit, $t(11)$
322 = 2.53, $P = .028$.

323 The increased position lead in congruent pursuit may be merely consequences of
324 decreased pursuit latency, as earlier pursuit initiation definitely leads to larger position
325 lead. We calculated the correlation across observers between the increased position
326 lead (congruent vs. incongruent) and the decreased pursuit latency (congruent vs.
327 incongruent). They were significantly correlated, but only for the first 200 ms of
328 pursuit. For example, in the [0 100] ms window, the position lead difference was
329 correlated with pursuit latency difference, $r = 0.71$ $P = .0099$. For [100 200] ms
330 window, $r = 0.68$, $P = .015$. However, 200 ms after finger onset (about 200-240 ms
331 after pursuit onset), the correlation disappeared. In the [200 300] ms window, they
332 were not correlated, $r = -0.017$. $P = .96$; in [300 400] ms window, $r = 0.011$, $P = .97$.
333 These results suggest that the position lead in congruent versus incongruent pursuit
334 was not merely a by-product of decreased pursuit latency, especially after the
335 open-loop phase of pursuit.

336

337 [-----insert Fig 5 here-----]

338

339 *Pursuit gain were larger in congruent pursuit.* The position measurement is not
340 optimal for pursuit quality as saccades also contribute to position data. Here we
341 computed finger/eye velocities and pursuit gain (eye velocity / finger velocity) after
342 excluding saccades in velocity traces (Fig 6). Due to anticipatory eye movement, the
343 gain was extremely high in the beginning (< 50 ms after finger onset). In the [100 300]
344 ms window, the gain was larger in congruent condition (mean = 0.92, SD = 0.11) than
345 that in the incongruent condition (mean = 0.83, SD = 0.19), $t(11) = 2.90$, $P = .014$.

346 The increased gain in congruent condition versus incongruent condition was due to a
347 higher eye velocity (congruent vs. incongruent: 27.1 ± 10.2 vs. 21.9 ± 9.6 deg/s; $t(11)$
348 $= 3.64$, $P = .004$), rather than a lower finger movement velocity (congruent vs.
349 incongruent: 30.4 ± 14.1 vs. 28.2 ± 15.1 deg/s; $t(11) = 1.09$, $P = .40$). Further, we
350 correlated the difference in gain and the difference in pursuit latency between
351 congruent and incongruent condition (Fig 6B), and observed a significant correlation,
352 $r = -0.60$, $P = .040$ ($r = -0.28$, $P = .41$ if the data point in the bottom right corner is not
353 considered). This suggests that same factors may lead to anticipatory pursuit initiation
354 and to the improvement in on-going pursuit control in the congruent condition.

355

356 [-----insert Fig 6 here-----]

357

358 *Saccades were fewer in congruent pursuit.* The number of saccades is another
359 measurement of pursuit performance. We plotted in Fig 7 the proportion of saccadic
360 trials in each 100 ms window. In a given time window (e.g., [-200 -100] ms), we
361 counted the number of trials that had at least one saccade within the time window, and
362 divided this by the total number of trials to calculate the proportion of saccadic trials.
363 The proportions were generally low, around 7.8% (SD = 6.0%) in congruent pursuit
364 and 10.7% (SD = 5.3%) in incongruent pursuit on average in the [0 300] ms window.
365 The congruent condition had significantly fewer saccadic trials than the incongruent
366 condition, $t(11) = -2.44$, $P = .033$.

367

368 [-----insert Fig 7 here-----]

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370 *Reversal delay was less in congruent pursuit.* Finally, we computed the time point
371 where the finger reversed direction (i.e., the peak in position trajectories) and
372 compared it to the time point where the eye reversed direction in individual trials.
373 Reversal delay was defined as the delay of eye reversal time relative to finger reversal
374 time (Fig 8). The delay was small, 1.9 ms on average in congruent pursuit (SD = 10.9

375 ms; not different from 0, $t(11) = 0.61$, $P = .56$) and 12.3 ms in incongruent pursuit
376 (SD = 16.3 ms; larger than 0, $t(11) = 2.61$, $P = .024$). The reversal delay was
377 significantly smaller in congruent pursuit than that in incongruent pursuit, $t(11) =$
378 -3.71 , $P = .004$. The decreased reversal delay in congruent pursuit versus incongruent
379 pursuit may be consequences of decrease pursuit latency. If so, we would expect a
380 positive correlation between the congruency effect in reversal delay and that in pursuit
381 latency. They were, however, not significantly correlated ($r = -0.47$, $P = .12$), and if
382 anything, the correlation is negative rather than positive as would have been expected.
383 The decreased reversal delay was thus not driven by the decreased pursuit latency.

384

385 [-----insert Fig 8 here-----]

386

387 The difference in pursuit quality between congruent and incongruent trials could
388 not be explained simply by a difference in finger motion speed. The average speed in
389 the outgoing leg of the motion in congruent trials (mean = 22.5 deg/s, SD = 8.4 deg/s)
390 did not differ from incongruent trials (mean = 21.7 deg/s, SD = 9.2 deg/s), $t(11) =$
391 0.79 , $P = .45$. In the first 200 ms after finger onset, finger speed in congruent trials
392 (mean = 16.2 deg/s, SD = 8.4 deg/s) also did not differ from incongruent trials (mean
393 = 14.8 deg/s, SD = 9.0 deg/s), $t(11) = 1.08$, $P = .20$.

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404 **Discussion**

405 Our main observation was an overall enhancement of smooth pursuit performance
406 when the eye and the hand moved in a congruent direction, compared to the case
407 when finger and eyes moved in opposite directions. The enhancement of performance
408 included reduced eye latency, increased lead of the eye in position, fewer saccades,
409 and reduced reverse latency. The effect could not be explained by the predictability of
410 the pursuit target, as directions of both eye and finger motions were constant in each
411 block of trials and thus completely predictable. The two conditions differed in the
412 low-level, directional congruency of the two movements. Hand motor commands
413 could be directly converted into eye motor commands in the congruent condition,
414 whereas the mapping was reversed in the incongruent condition. This result suggest
415 that the specific signal that leads to finger movement execution contributes to
416 eye-hand coupling in finger tracking.

417 A few previous studies examined finger pursuit in incongruent conditions similar
418 to ours. In their setups, the hand movements were monitored and were reproduced on
419 a computer screen in near real time. Domann, Bock and Eckmiller (1989) reported
420 that human participants as well as primates are capable of tracking a target that moves
421 oppositely to the hand. They reported close to zero eye latencies in both congruent
422 and incongruent conditions, but did not explicitly compare them. They concluded that
423 motor intention signals drive pursuit in finger tracking. Vercher, Quaccia and Gauthier
424 (1995) subsequently reported similar results in incongruent pursuit blocks. They also
425 tested the condition where the mapping of the target to the hand was randomized
426 across trials. They found that in incongruent trials the eye started to move in the
427 direction of the arm for the first ~140 ms. Afterwards, the eye reversed direction to
428 catch up with the visual tracking target. In a preliminary report, Spitschan and
429 Vishwanath (2011) varied hand-target gain and observed the best pursuit performance
430 for the 1:1 direct mapping, compared to the reverse 1:1 and other gain conditions.
431 Independently of the target speed, they also reported better performance (in terms of
432 pursuit gain and number of saccades) when the target was controlled by the finger
433 movement compared to when the target motion was controlled externally. A recent

434 preliminary report (Kowler et al., 2015) also found anticipatory pursuit eye
435 movements in incongruent tracking.

436 In general, previous studies have shown that the pursuit system can anticipate the
437 future target movement even if the mapping is incongruent. This is consistent with our
438 results, as we observed very low eye latency, few saccades and a small reverse delay
439 in the incongruent condition. High-level signals related to motor intention/decision
440 are used for the eye to anticipate finger movements. However, our study further
441 showed that the anticipation was enhanced even further if the target motion was
442 congruent with the finger motion, compared to incongruent mapping. This means that
443 predictive signals tightly bound to motor execution also play a role in finger tracking.
444 While this notion has been suggested before (e.g., Vercher et al. 1996), to our
445 knowledge it has not been tested directly by dissociating motor execution from motor
446 intention while maximizing target motion predictability.

447 Vercher, Quaccia and Gauthier (1995) observed an adaptation effect after the
448 mapping was reversed. In their study, in the first few trials, the gaze was initiated in
449 the direction of hand, rather than the visual target. In less than 10 trials, participants
450 learned the reversed mapping and initiated pursuit with zero latency. The
451 learning/adaptation effect was also observed in Domann, Bock and Eckmiller (1989)'s
452 study. They trained non-human primates to track hand movements with gaze in
453 reversed mapping condition, and observed decreasing pursuit latencies with training.
454 In addition, they observed a bimodal distribution in pursuit latency, one visual-driven
455 component with 100-200 latency and one non-visual driven component with 0 latency.
456 The learning effect was associated with increased occurrence of non-visual driven
457 component and decreased occurrence of visual driven component. In the present study,
458 there might have been some adaptation effect in the incongruent condition. The
459 adaptation, however, was not complete and the congruency effect held throughout the
460 experiment. Previous studies in fact were not designed to test the congruency effect
461 and did not explicitly report the comparison. Our results complemented these studies
462 by showing that the adaptation to incongruent mapping does not easily abolish the
463 incongruency cost. Domann, Bock and Eckmiller (1989) in addition showed the

464 bimodal distribution in the pursuit latency while training non-human primates to do
465 the reversed-mapping tracking task. Neither our study nor Vercher, Quaccia and
466 Gauthier (1995) found bimodality. One possible explanation lies in the difference
467 between human participants and non-human subjects. Humans may instantly learn the
468 reversed mapping in few trials, while non-human primates have to take days of
469 gradual training, which resulted in a co-existence of both components.

470 One alternative explanation for the decreased pursuit performance is that
471 attention allocated to the pursuit system might be reduced in incongruent pursuit, as it
472 is likely that the hand movement in the opposite direction would require a certain
473 amount of attentional resource. The effect of dividing attention on smooth pursuit eye
474 movements has been investigated in a few studies. Van Gelder et al (1995) and
475 Kathmann, Hochrein and Uwer (1999) added a secondary auditory task on top of the
476 pursuit task. They did not find any dual task interference, if anything tracking error
477 during pursuit decreased in the dual-task condition. Later, Hutton and Tegally (2005)
478 showed that a more demanding secondary task, i.e., tapping a fixed number sequence
479 with the finger, reduced pursuit gain and increased tracking error. Easy secondary
480 tasks neither increased nor decreased pursuit performance. Recently, Seya and Mori
481 (2015) used a manual reaction time task during smooth pursuit, and set different
482 deadlines (300, 400 or 500 ms) for the manual response. They found significant
483 increased tracking error with a 300-ms deadline, but no difference between 400-ms
484 and 500-ms deadlines. These results consistently suggest that smooth pursuit
485 performance is largely unharmed until the secondary task becomes very demanding.
486 The finger movements required from our observers were very repetitive, stereotyped
487 and the timing constraints were quite loose, meaning that the task was far from
488 attentionally demanding. Also notice that we found a decrease in eye latency, among
489 other performance measures, in the incongruent pursuit. Souto and Kerzel (2008)
490 found that divided attention particularly affected close-loop pursuit, but it had little
491 effect on smooth pursuit latency and early open-loop response. Overall, it seems
492 rather unlikely that the comparatively worse pursuit performance in incongruent
493 pursuit is due to divided attention.

494 Our findings have implications for the debate on models of eye-hand coordination
495 in finger tracking. Two prominent proposals are the common controller model (Bock,
496 1987) and the mutual coordination system (Lazzari et al. 1997). In our study, the
497 motor execution signals, which directly originate from the hand motor system, was
498 found be able to influence the pursuit performance. This seems to support the mutual
499 coordination system hypothesis, as the common controller model assumes no direct
500 interactions between two systems (Scarchilli and Vercher, 1999). Our results fit well
501 with recent neurophysiology results showing mutual influences between the hand
502 movement system and eye movement system under coordination. Yttri, Liu and
503 Snyder (2013) recorded from lateral intraparietal area (LIP), a region associated with
504 saccadic eye movements. They reported that, whereas inactivation of LIP did not
505 affect hand reach movements made in isolation, the inactivation did impair reach
506 movements when made in coordination with saccades. It suggests that saccade system
507 does interact with hand reach movement system under eye-hand coordination.
508 Similarly, inactivation of the parietal reach region had an influence on coordinated
509 saccades, but not saccades executed in isolation (Hwang et al. 2014; but see Yttri et al.
510 2014). This study shows that reach system interacts with saccade system when they
511 are coordinated. While these studies dealt with saccade/reach movements, we recently
512 (Chen, Valsecchi and Gegenfurtner, 2016) showed that lateralized readiness potentials
513 (LRPs) predict smooth pursuit latency in finger tracking. As LRPs are motor
514 preparation signals originating mainly from the primary motor cortex (Coles 1989; de
515 Jong et al. 1988), this finding suggest a direct interaction by linking motor commands
516 responsible for finger movements with onset of the pursuit system. The present study
517 is consistent with this finding and extends it by showing that even a simple change in
518 the mapping between finger and pursuit target motion, such as mirroring, prevents the
519 oculomotor system from fully exploiting the interactive signals attached to finger
520 motor commands.

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525

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619

620 **Figure captions:**

621

622 Fig 1. The diagram of device used in the experiment. The example setting shows the
623 incongruent condition, where the tracking target is attached to the back side of the belt.
624 As a result, the target moves always in the opposite direction when the finger moves.
625 Note that the device and the hand were occluded, while only the tracking target was
626 visible to the observer.

627

628 Fig 2. Average position (top) and average velocity (bottom) for the eye and finger for
629 one example observer in the congruent (A) and incongruent (B) condition.

630

631 Fig 3. (A and B) Eye onset time plotted against finger onset time for individual
632 participants in the Congruent (A) and Incongruent (B) conditions. Eye onset was
633 earlier than finger onset in A but not in B. (C) Eye latency in incongruent pursuit
634 plotted against eye latency in congruent pursuit for individual participants. Eye
635 latency was smaller in congruent pursuit. (D) Frequency plot of eye latencies in all
636 trials of one example participant. Eye latency was overall reduced in the congruent
637 condition. The cross in (A-C) shows the average value \pm SEM.

638

639 Fig 4. Eye latency in congruent and incongruent condition with increasing number of
640 trials. Some adaptation may take place in the incongruent condition. The congruency
641 effect, however, still held even in the last 40 trials. Error bars indicate \pm SEM.

642

643 Fig 5. (A) Position lead of the eye relative to the finger in congruent pursuit and
644 incongruent pursuit. (B) Temporal lead of the eye relative to the finger (asynchrony
645 between eye and finger reaching a given position). Shaded areas indicate \pm SEM.

646

647 Fig 6. (A) The pursuit gain for congruent and incongruent condition. The gain was
648 larger in the congruent condition. Shaded areas indicate \pm SEM. (B) The increased
649 gain in congruent versus incongruent condition was correlated with the decreased
650 pursuit latency, suggesting similar underlying factors for anticipatory pursuit initiation
651 and improvement in on-going pursuit control.

652

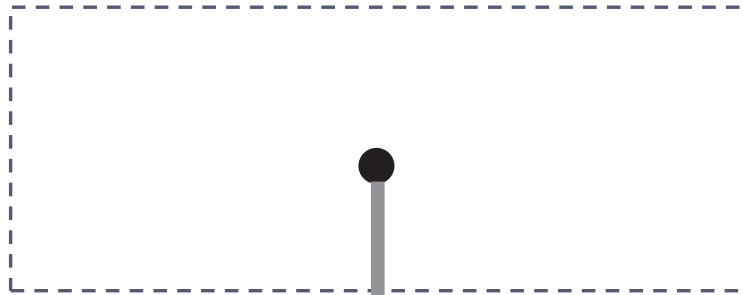
653 Fig 7. Proportion of trials that have saccades for every 100 ms time window,
654 separately for the congruent and incongruent conditions. Error bars indicate \pm SEM.

655

656 Fig 8. Reversal delay in congruent and incongruent pursuit. Open circles indicate
657 individual participants. The cross shows the average value and \pm SEM.

658

Visible to
observer



Occluded

