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1 Eye-hand coordination all the way: from discrete to continuous 2 hand movements

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6 *Running head:* Eye-hand coordination all the way

7 8 **ABSTRACT**

9 The differentiation between continuous and discrete actions is key for behavioral
10 neuroscience. Although many studies have characterized eye-hand coordination during
11 discrete (e.g. reaching) and continuous actions (e.g. pursuit tracking), all these studies were
12 conducted separately, using different setups and participants. In addition, how eye-hand
13 coordination might operate at the frontier between discrete and continuous movements
14 remains unexplored. Here we filled these gaps by means of a task that could elicit different
15 movement dynamics. Twenty-eight participants were asked to simultaneously track with their
16 eyes and a joystick a visual target that followed an unpredictable trajectory and whose
17 position was updated at different rates (from 1.5 to 240 Hz). This procedure allowed to
18 examine actions ranging from discrete point-to-point movements (low refresh rate) to
19 continuous pursuit (high refresh rate). For comparison, we also tested a manual tracking
20 condition with the eyes fixed, and a pure eye tracking condition (hand fixed). The results
21 showed an abrupt transition between discrete and continuous hand movements around 3 Hz
22 contrasting with a smooth tradeoff between fixations and smooth pursuit. Nevertheless, hand
23 and eye tracking accuracy remained strongly correlated, with each of these depending on
24 whether the other effector was recruited. Moreover, gaze-cursor distance and lag were smaller
25 when eye and hand performed the task conjointly than separately. Altogether, despite some
26 dissimilarities in eye and hand dynamics when transitioning between discrete and continuous
27 movements, our results emphasize that eye-hand coordination continues to smoothly operate
28 and support the notion of synergies across eye movement types.
29

30 **NEW & NOTEWORTHY**

31 The differentiation between continuous and discrete actions is key for behavioral
32 neuroscience. By using a visuomotor task in which we manipulate the target refresh rate to
33 trigger different movement dynamics, we explored eye-hand coordination all the way from
34 discrete to continuous actions. Despite abrupt changes in hand dynamics, eye-hand
35 coordination continues to operate via a gradual tradeoff between fixations and smooth pursuit,
36 an observation comforting the notion of synergies across eye movement types.
37

38 *Keywords:* eye-hand coordination; humans; manual tracking; point-to-point reaching; smooth
39 pursuit; saccades; fixations

40 INTRODUCTION

41 In everyday life, eye-hand coordination is essential to perform a large panel of actions (1–
42 3). These actions are typically separated into discrete and continuous ones (4, 5). Discrete
43 tasks rely on movements of short duration (typically <1s) that mostly place the goal of action
44 at the end and continuous tasks rely on movements of longer duration in which a certain goal
45 must be fulfilled throughout the entire movement. The differentiation between continuous and
46 discrete actions is key for behavioral neuroscience (6) as these two types of movement are
47 supported by partly distinct neurophysiological substrate (7) and are generally associated with
48 different timing mechanisms (6) and different levels of reliance on feedforward and feedback
49 processes (8, 9). Moreover, if neurophysiological evaluation of eye-hand coordination
50 emphasizes the key role of the posterior parietal cortex during discrete actions (10–13), it is
51 the contribution of the cerebellum that is highlighted during continuous ones (14–16). At the
52 lab, conventional reaching (i.e. in the absence of perturbations/obstacles), in which hand
53 motor command is essentially programmed before movement initiation, offers a convenient
54 proxy to study eye-hand coordination in discrete movements (17–20). In contrast, tracking
55 tasks, in which accurate performance is required from movement initiation till movement
56 completion, and whereby online adjustments in hand movements are a constant requirement,
57 offer a convenient proxy to study eye-hand coordination in continuous movements (15, 21–
58 24). Although a large body of studies has aimed to investigate eye-hand coordination in
59 discrete and continuous actions, to our knowledge these were always studied separately,
60 namely by using different behavioral variables, setups, and participants, which incidentally
61 prevents fair comparison between the two. Here, not only we propose to fill this gap, but we
62 also wish to characterize eye-hand coordination for movements lying at the frontier between
63 discrete and continuous actions. We reason that, because discrete and continuous movements
64 rely on (partly) separate neural pathways and control mechanisms, it is not obvious that the

65 principles driving eye-hand coordination in one context will generalize to the other, leaving
66 open the type of coordination that will emerge at their frontier.

67 Before addressing this issue further, we propose to review several key findings relative
68 to eye-hand coordination in reaching and tracking movements and to point the separate
69 contribution of eye movements (fixations, saccades, and smooth pursuit) into each of these.
70 During reaching tasks, discrete movement of the hand relies on a precise succession of
71 fixations and saccades. Such eye-hand coordination is evidenced by several key findings.
72 First, before the hand moves toward a spatial location, a fast saccadic movement of the eye is
73 initiated toward that same location (20, 25, 26). Still, despite the fact the reaction time of the
74 eye is typically faster than that of the hand, the latencies of both effectors are correlated
75 arguing for shared processes (27–29). Second, even after the saccade has reached the target, it
76 is difficult to move the eye away before the hand has also reached the target (30, 31). It is
77 advocated that foveating the target location promotes the accuracy of the reach, not only by
78 facilitating the transformation from a retinotopic to a body-centered frame of reference (32,
79 33), but also by promoting guidance of the hand in the vicinity of the target (26, 34–37).

80 Unlike reaching, during tracking tasks, visual guidance of continuous hand movements
81 relies on a succession of smooth pursuit episodes and catch-up saccades allowing gaze to stay
82 in the vicinity of the moving target (38–40). Despite that difference, several key findings
83 demonstrate the persistence of an intimate relationship between eye and hand in these
84 continuous actions. First, when participants are required to keep their eyes fixed manual
85 tracking accuracy is substantially impaired (22, 41). Second, eye movements are not identical
86 when simultaneously tracking a moving target with the hand or with the eyes only. Indeed, in
87 comparison to eye tracking alone, concurrent eye hand tracking induces fewer catch-up
88 saccades and enhances smooth pursuit as evidenced by higher velocity and gain (21, 23, 24,
89 42). Note however, that this improvement in smooth pursuit is accompanied by increased eye-

90 target distance and/or lag (21, 23, 41, 43). Third, during concurrent eye and hand tracking,
91 movement of both effectors are interrelated, both in the temporal and spatial domain. This is
92 evidenced by the fact that the temporal lag of eye and hand with respect to the target are
93 correlated, and that the observed gaze-cursor distance is smaller than what would be expected
94 from two independent effectors (44). Finally, participants who tend to track better the target
95 with their eyes are also those that track better the target with their hand (44).

96 Altogether, regardless of whether humans perform discrete reaching movements or
97 continuous tracking ones, there is compelling evidence that eye and hand actions share some
98 common input. However, because in each case eye-hand coordination was evaluated using
99 different protocols and dependent variables, not only their comparison is challenging, but it
100 also makes intractable the exploration of eye-hand coordination for movements lying between
101 discrete and continuous ones. Although a first motivation for the current study is to address
102 these shortcomings, the fact that reaching and tracking differ markedly with respect to the
103 contribution of fixations, saccades, and smooth pursuit (1) is also a strong incentive. Indeed,
104 because there is general agreement that these eye movements are subtended by partly
105 overlapping neural circuitries facilitating the emergence of synergies between them (40, 45–
106 48), we reason that exploring eye movements at the frontier between discrete and continuous
107 movements offers new opportunities to assess the extent to which fixations, saccades, and
108 smooth pursuit can smoothly cooperate.

109 To address all these issues, we introduce a novel task that can elicit a wide range of
110 hand movements all the way from discrete to continuous ones. During that task participants
111 must track a target whose initial trajectory is pseudorandom and continuous (combination of
112 several sinusoids), but whose visual position can be refreshed at various frequencies. When
113 that refresh frequency is low (discrete target motion), we expect participants to produce
114 essentially point-to-point (discrete) hand movements in conjunction with saccades and

115 fixations. In contrast, when this frequency is high (continuous target motion), we expect
116 participants to produce rather continuous pursuit hand movements in conjunction with smooth
117 pursuit eye movements and catch-up saccades. As reported by others, we expect to observe
118 reliable eye-hand coordination in each of these extreme conditions, however it is unclear what
119 kind of eye-hand coordination (if any) can be found for movements lying between these two
120 extremes. When performing back and forth movements between two fixed targets at
121 increasing (or decreasing) frequencies, the transition between discrete and continuous
122 movements occurred around 2 Hz for whole arm (49) or index finger movement (6).
123 Assuming a clear (abrupt) transition between discrete and continuous hand movement in our
124 task, a first possibility is that below the critical frequency participants should rely solely on
125 fixations and saccades, whereas above that frequency they should rely uniquely on catch-up
126 saccades and smooth pursuit. Alternatively, if the transition between the discrete and the
127 continuous regime is gradual, one may expect participants to rely simultaneously on fixations,
128 saccades, and smooth pursuit episodes for intermediate frequencies, an observation that would
129 extend the notion of synergies across eye movement types (40, 45, 46). Furthermore, no
130 matter whether the transition in hand movements is abrupt or gradual, one may wonder
131 whether eye-hand coordination suffers from instabilities inherent to transitions (50, 51).
132 Finally, to better assess the mutual influence between eye and hand actions, our initial task
133 (manual tracking with the eyes free) is contrasted with a pure eye tracking task (i.e. no manual
134 tracking involved), as well as a pure manual tracking task (i.e. eyes being fixed). As will be
135 seen, although a rather abrupt transition between discrete and continuous hand movements
136 was observed, it was accompanied by a much more gradual transition in eye movements
137 (allowing the coexistence of fixations, saccades and smooth pursuit), with only subtle
138 impairments in eye-hand coordination in the vicinity of the transition.

139

165 technical issues, measurements were taken from the left eye in four participants. For each
 166 participant, a calibration procedure was conducted at the beginning of the experiment using a
 167 fixation grid composed of nine known locations (22, 53). This procedure was repeated before
 168 each block of trials (i.e. every 32 trials).

169

170 *Experimental Design*

171 Throughout the experiment, participants had to perform a task that consisted in tracking
 172 a moving target with their right hand and/or the eyes. In all our experimental conditions, trials
 173 lasted for 10 s, and target motion was determined by a combination of sinusoids: two along
 174 the frontal axis, and two on the sagittal axis (21, 22). The following equations and parameters
 175 (Table 1) were used to generate four target trajectories:

$$176 \quad x_t = A_{1x} \cos \omega t + A_{2x} \cos (h_x \omega t - \varphi_x) \quad (1)$$

$$177 \quad y_t = A_{1y} \sin \omega t + A_{2y} \sin (h_y \omega t - \varphi_y) \quad (2)$$

Trajectory	A1x (cm)	A2x (cm)	Harmonic x	Phase x (°)	A1y (cm)	A2y (cm)	Harmonic y	Phase y (°)
1	5	5	2	45	5	5	3	-135
2	4	5.1	3	-60	4	5.2	2	-135
3	5	5	3	90	3.4	5	2	45
4	5.1	5.2	2	-90	4	5	3	22.5

178
 179 **Table 1.** Target trajectory parameters

180 All these four trajectories were selected based on their similarity in terms of mean
 181 tangential velocity (16 cm/s) and mean eccentricity (± 6 cm). To manipulate the
 182 discrete/continuous aspect of target motion, we varied the time interval at which the target
 183 position was updated on the screen, somehow mimicking a stroboscopic effect. This
 184 procedure ensured that the target remained always visible on the screen, but as the refresh rate
 185 increased, target jumps became smaller and more frequent (see examples of discretization for
 186 two of the four trajectories in Figure 2). Eight refresh rates were tested: 1.5, 2, 2.5, 3, 3.5, 4, 8
 187 and 240 Hz (the latter being the maximum refresh rate of our screen, as employed in our

188 previous studies). These frequencies were selected based on pilot data to cover a wide variety
189 of hand movements ranging from discrete to continuous movements.

190 (Please insert Figure 2 about here)

191 Participants completed the tracking task under each of the three following conditions. In
192 the EYE-HAND (EH) condition participants were instructed to move the joystick with their
193 right hand so as to keep, at all times, the cursor (red disk, 0.5° in diameter) as close as
194 possible to the target (blue dot, 0.5° in diameter). No explicit instructions were given
195 regarding eye movements. In the HAND only (H) condition participants were asked to
196 perform the same pursuit task with the joystick, but they were instructed to keep their gaze on
197 a yellow cross positioned at the center of the screen (see (22) for a similar design). In the EYE
198 only (E) condition, while they no longer held the joystick (cursor being turned off),
199 participants were asked to always keep their eyes as close as possible to the target.

200 Each participant completed a total of 96 trials organized in three sessions (32 trials
201 each), one for each version of the tracking task (E/H/EH). The order of sessions was
202 counterbalanced across participants. Each session was composed of 8 successive blocks (one
203 per target frequency) of 4 trials each (one per trajectory). The order of trajectories within each
204 frequency block, as well as the order of frequency blocks within each session, were
205 randomized across participants. However, for a given participant, the order of trajectories and
206 frequencies was kept constant across the three sessions.

207

208 *Data Analysis*

209 Data were analyzed with Matlab (2022b version). A total of 2688 trials were collected
210 over our 28 participants, and all these trials were kept for analyses (no trial was excluded).
211 For all our analyses, the first second of each trial was excluded to prevent from initial
212 transients due to initial cursor positioning (21, 56). A first step consisted in evaluating the

213 accuracy of eye and hand tracking performance. To achieve this, the Euclidean distance
214 between gaze/cursor and target position was computed at each instant and then averaged over
215 the whole trial (last 9 seconds). Although that procedure is consistent with the requirement to
216 always stay as close as possible to the target, it is not intended to focus on positional errors
217 found at the end of each eye/hand discrete movement (see examples in Figure 5). The
218 temporal lag between gaze/cursor and target was computed using a method that cross-
219 correlates the associated signals along both the vertical and horizontal axis (21). A positive
220 lag indicates that the effector (eye/hand) was lagging on the target. This assessment of the
221 gaze/cursor lag is not intended to faithfully capture the latency of eye and hand discrete
222 movements at each target jump, but rather to provide an overall estimate of the temporal
223 relationship between eye/cursor and target motion over the entire course of the trial.

224 A next step consisted in characterizing the discrete/continuous nature of hand
225 movements (see Figure 3). We addressed this by examining the phase portraits between
226 cursor tangential velocity and its acceleration. We reasoned that when participants generate
227 discrete hand movements, the time interval between the termination of one movement and the
228 initiation of a new one should lead to simultaneous low cursor velocity and acceleration (see
229 Figure 3A and B). In contrast, if hand movement remains continuous, not only cursor
230 tangential velocity should rarely approach zero, but also low acceleration should not be
231 associated with low velocity (see Figure 3D and E). Altogether, this asymmetry in behavior
232 leads to structural differences in velocity acceleration phase portraits (see Figure 3C and F).
233 We exploited this feature by contrasting, for each trial, the time spent by the cursor in two
234 distinct regions of the velocity-acceleration phase portrait (using low pass filtered signals at
235 20 Hz). A first region (R1), intended to capture the discrete nature of hand movement,
236 consisted in a rectangle where both cursor velocity and acceleration were low ($0 < vel < 10$
237 cm/s , $-100 < acc < +100 cm/s^2$). A second region (R2), intended to capture the continuous

238 nature of hand movement, consisted in a rectangle in which similar cursor acceleration was
239 intended ($-100 < \text{acc} < +100 \text{ cm/s}^2$), but this time requiring higher cursor velocity ($10 < \text{vel} < 20$
240 cm/s) as expected from mean target velocity in the continuous case (16 cm/s). To reduce the
241 number of dependent variables, the time spent by the cursor in R2 was subtracted from R1.
242 We reasoned that a positive value ($R1 > R2$) is indicative of a rather discrete regime, whereas a
243 negative value ($R1 < R2$) indicates a rather continuous regime.

244 **(Please insert Figure 3 about here)**

245 A last step consisted in partitioning eye signals into blinks, saccades, fixations, and
246 smooth pursuit episodes. Blinks were detected automatically using the loss of pupil signal, but
247 subsequently double-checked by visual inspection. This procedure led to the removal of
248 0.36% of eye recordings. The next stage consisted in identifying saccades based on eye
249 tangential velocity and acceleration. To achieve this X and Y positional eye signals were first
250 low pass filtered with a 4th order Butterworth using a cutoff frequency of 25 Hz. Tangential
251 eye velocity and acceleration were calculated from these signals. Initiation and termination of
252 saccades were identified using thresholds of 20 deg/s for velocity and 1200 deg/s² for
253 acceleration. Following this procedure, each trial was visually inspected to ensure the
254 identification of smaller saccades. Once blinks and saccades were identified, we analyzed the
255 remaining eye segments to tease apart fixations and smooth pursuit episodes. Based on
256 previous studies that focused on ocular event detection (57, 58), we implemented an algorithm
257 using spatial dispersion of gaze that was fed by low pass filtered eye signals (4th order
258 Butterworth, 25 Hz cutoff frequency). For each eye segment that was not identified as a blink
259 or a saccade, our algorithm computed a 95% confidence ellipse using the XY position data,
260 and then computed the ratio between the major and the minor axis of the ellipse. We reasoned
261 that whenever this ratio was large (longer dispersion along one axis), that segment was a
262 smooth pursuit episode (see Figure 4A), conversely when this ratio was close to 1 (same

263 dispersion along the two axes), that segment was a fixation (see Figure 4B). To further refine
264 this identification technique, we also considered the Euclidian distance covered by the eye
265 between the first and the last data point of each segment. We reasoned that fixation should be
266 associated with smaller distance than smooth pursuit episodes. Altogether, we set that
267 whenever that distance did not exceed 1° , and that the ellipse ratio was below 8, that segment
268 was automatically reconsidered as a fixation. If the duration of the remaining segments was at
269 least 100 ms, they were considered as smooth pursuit episodes. For the current dataset, this
270 method appeared more reliable than methods using velocity only algorithms (58, 59).

271 **(Please insert Figure 4 about here)**

272 To characterize eye-hand coordination we examined to what extent eye and hand
273 followed the target independently. To achieve this, for each target trajectory and refresh rate,
274 we compared the eye-cursor lag and distance when these two effectors performed the task
275 concurrently (EH) to the virtual lag and distance that would have been obtained if both
276 effectors had kept the same behavior as when performing the task in isolation. To account for
277 the latter case, for each participant and each of the 4 trajectory patterns, we combined hand
278 and eye signals generated during the E and H conditions. We reasoned that ‘true’ eye-hand
279 coordination should lead to smaller eye-cursor lag/distance in the EH condition compared to
280 our composite condition (E+H).

281 *Statistical analyses*

283 In most cases, each dependent variable was submitted to a two-way repeated measures
284 ANOVA that assessed the effect of target frequency (8 levels: 1.5, 2, 2.5, 3, 3.5, 4, 8, and 240
285 Hz) and type of tracking (up to 3 levels: EH/E/H). Whenever necessary we used Newman-
286 Keuls post-hoc comparisons. A conventional 0.05 significance threshold was used for all the
287 analyses.

288

289 **RESULTS**

290 *Typical trials*

291 Figure 5 presents typical eye and hand signals collected from three participants during EH
292 trials performed at low, intermediate, and high target refresh rates. As can be seen, hand and
293 eye movement dynamics change substantially depending on target frequency. At the lowest
294 frequency, hand movement consists of a succession of discrete movements, accompanied by a
295 series of saccades and fixations for the eye. In contrast, at the highest frequency, hand
296 movement appears rather continuous, and is complemented by saccadic and smooth pursuit
297 eye movements. Below we analyze quantitatively these changes in hand and eye movements
298 with two objectives. First, we try to characterize the nature of these transitions (slow/abrupt).
299 Second, we evaluate whether these transitions are affected by the presence/absence of the
300 other effector. Then we address the associated changes in hand and eye tracking performance,
301 along with the possible changes in eye-hand coordination.

302 (Please insert Figure 5 about here)

303 *Hand movement dynamics*

304 Figure 6A shows the heatmap of velocity-acceleration phase portraits for each target
305 frequency in the EH condition. As can be seen, at the lowest frequencies warm colors are
306 essentially located on the left side of the phase portraits (in R1), thereby reflecting the discrete
307 nature of hand movements (with frequent moments combining low velocity and acceleration).
308 In contrast, at the highest target frequencies, warm colors are positioned on the right side of
309 the phase portraits (toward R2). Visual inspection suggests a rather abrupt transition between
310 discrete and continuous hand movements (around 3 Hz). Rather similar observations are
311 obtained when examining heatmaps associated with manual tracking under the eyes fixed
312 condition (see Figure 6B), except that the transition occurs at a lower target frequency (around
313 2.5 Hz). To examine this issue in more detail, we quantified the time spent in regions R1 and

314 R2 as function of target frequencies and conditions (EH vs H). Two-way ANOVA of the time
315 difference (R1-R2) revealed a main effect of FREQUENCY ($F(7,189) = 272.7, p < 0.001$),
316 CONDITION ($F(1,27) = 6.028, p = 0.028$) and a FREQUENCY by CONDITION interaction
317 ($F(7,189) = 2.135, p = 0.042$). The effect of FREQUENCY was consistent with a switch in
318 sign across our frequency range (+2.57 s at 1.5 Hz vs. -0.934 s at 240 Hz) matching well the
319 tendency to perform discrete movements at low frequency and continuous ones at high
320 frequency. The post-hoc of the interaction revealed significantly lower indices in H compared
321 to EH but only for the intermediate frequencies, namely at 2.5 Hz (0.482 vs 0.915 s,
322 $p = 0.015$) and 3 Hz (-0.016 vs -0.384 s, $p = 0.037$). These latter results support the view that
323 gaze fixation facilitates the transition from discrete to continuous hand movements by means
324 of a lower critical frequency (EH = 3 Hz, H = 2.5 Hz).

325 (Please insert Figure 6 about here)

326 *Eye movement types*

327 In Figure 7A, B, and C, we present the fraction of time spent under fixations, smooth
328 pursuit, and saccades, as a function of target frequency in both the EH and E conditions. As
329 can be seen, the contribution of each eye movement type varied substantially with target
330 frequency. Notably, in both EH and E we observe an extensive and gradual trade-off between
331 fixations and smooth pursuit. At low target frequency, fixations dominate over smooth pursuit
332 (observed marginally), but at high target frequency we find the opposite trend with smooth
333 pursuit dominating over fixations (virtually absent). Indeed, when target frequency switched
334 from 1.5 to 240 Hz, averaged across EH and E, the contribution of fixation was reduced by
335 almost a factor of 20 (switching from 77.5 to 4.0%; see Figure 7A), whereas smooth pursuit
336 contribution increased by almost a factor of 20 (switching from 4.1 to 78.8%; see Figure 7B).
337 These two observations were corroborated by main effects of FREQUENCY
338 ($F(7,189) > 335.8, p < 0.001$). In contrast, the contribution of saccades appeared more stable

339 across target frequencies. Although a main effect of FREQUENCY was also observed in this
340 case ($F(7,189) = 55.3, p < 0.001$), fluctuations in the contribution of saccade never reached a
341 factor of 2 (see Figure 7C). The contribution of each eye movement type depended on the
342 presence/absence of concurrent hand tracking as revealed by a main effect of CONDITION in
343 each case ($F(1,27) > 16.34, p < 0.001$). Averaged across frequencies, eye-alone tracking led to
344 a higher percentage of fixations (E=54% vs. EH=50%) and saccades (E=22% vs. EH=20%)
345 but resulted in a lower percentage of smooth pursuit (E=24% vs. EH=30%). Altogether, these
346 effects retard the transition from fixations (and saccades) to smooth pursuit with increasing
347 target frequency. Finally, in Figure 7D and E, we collapse the information provided in panel
348 A, B, and C, into stacked histograms to better appreciate the respective contribution of
349 fixations, saccades, and smooth pursuit in the EH and E condition. These histograms
350 emphasize that, in contrast to the rather abrupt changes found in hand movement dynamics
351 (see Figure 6), changes in eye movement types were more gradual, allowing the coexistence
352 of fixations, saccades, and smooth pursuit during intermediate target frequencies.

353 (Please insert Figure 7 about here)

354 *Accuracy of hand and eye tracking*

355 As shown in Figure 8, the accuracy of hand and eye tracking improved substantially as
356 target frequency increased. Moreover, most of our indices showed that this accuracy was
357 influenced by whether the other effector was simultaneously engaged in tracking. We propose
358 first to concentrate on hand tracking performance, that is on conditions EH and H. Regarding
359 cursor-target distance (see Figure 8A), the ANOVA showed a main effect of FREQUENCY
360 ($F(7,189) = 617.9, p < 0.001$), CONDITION ($F(1,27) = 44.45, p < 0.05$) and FREQUENCY
361 by CONDITION interaction ($F(7,189) = 35.29, p < 0.001$). The effect of FREQUENCY is
362 consistent with an increase in hand-tracking performance as target frequency increases,
363 leading to a cursor-target distance about 2 times smaller at 240 Hz compared to 1.5 Hz (2.27
364 vs. 4.86 cm, values being averaged across EH and H). The effect of CONDITION is

365 consistent with the fact that hand tracking accuracy decreased under gaze fixation. Still post-
366 hoc of the interaction indicates that this effect was significant only at the highest frequencies,
367 namely from 4 Hz up to 240 Hz ($p < 0.05$), suggesting that preventing eye movements was
368 detrimental only at the highest target frequencies. The analysis of cursor-target lag (see Figure
369 8B) also supports the view that hand tracking performance increases with target frequency
370 ($F(7,189) = 710.8$, $p < 0.001$). Specifically, averaged across EH and H, the cursor-target lag
371 decreased from 337 ms at 1.5 Hz to 63 ms at 240 Hz, a 5 times difference. There was also a
372 FREQUENCY by CONDITION interaction ($F(7,189) = 6.48$, $p < 0.001$), but no main effect
373 of CONDITION ($F(1,27) = 0.056$, $p = 0.81$). Post-hoc of the interaction only revealed a
374 marginal difference between EH and H conditions at 240 Hz ($p = 0.061$) suggesting that, in
375 contrast to spatial precision, gaze fixation did not alter much the temporal precision of hand
376 movements. These contrasting observations suggest that the greater cursor-target distance
377 induced by gaze fixation under high frequencies (see right side of Figure 8A) does not stem
378 from increased latency in visuomotor feedback loops minimizing tracking error but rather
379 from weaker sensitivity to tracking error (i.e. lower feedback gain).

380 (Please insert Figure 8 about here)

381 To a large extent eye tracking performance mirrored hand tracking performance. Indeed,
382 not only eye tracking accuracy improved with target frequency, but it was also influenced by
383 what the other effector was doing (staying still or tracking). At the bottom of Figure 8, we
384 present the eye-target distance (panel C) and lag (panel D) as a function of target refresh rate
385 in the EH and E condition. Two-way repeated measure ANOVA revealed a main effect of
386 FREQUENCY for both the eye-target distance ($F(7,189) = 663.5$; $p < 0.001$) and lag
387 ($F(7,189) = 409$; $p < 0.001$). When switching from 1.5 to 240 Hz, averaged across EH and E,
388 eye-target distance decreased from 3.2 to 1.4 cm, and eye-target lag from 185 to 50 ms. Main
389 effects of CONDITION were also observed at the spatial ($F(1,27) = 35.53$; $p < 0.001$) and

390 temporal level ($F(1,27) = 115.6, p < 0.001$). Briefly, eye tracking performance was degraded
391 during dual tracking compared to eye-tracking alone, with a 12% increase in cursor-target
392 distance (3.07 vs. 2.75 cm), and a 24 ms increase in eye-target lag. Regarding eye temporal
393 accuracy, the FREQUENCY by CONDITION interaction was significant ($F(7,189) = 5.27,$
394 $p < 0.001$), with post hoc indicating that differences between E and EH were significant for all
395 frequencies ($p < 0.01$). However no interaction was observed regarding eye-target distance
396 ($F(7,189) = 1.69; p = 0.114$). Overall, these analyses show that eye and hand exhibit greater
397 temporal and spatial accuracy with higher target refresh rate, and that their tracking
398 performances are interdependent. We explore further this latter aspect in the next section.

399

400 *Eye-hand coordination*

401 The degree of interdependence between eye and hand movements was first evaluated by
402 assessing the correlation between eye and hand tracking performance in the EH condition
403 over the 8 target frequencies. As suggested by Figures 8A and C, the correlation between eye-
404 target distance and cursor-target distance was significant not only for group data ($R = 0.92, p$
405 $= 0.001$) but also within participant ($R = 0.89 \pm 0.06; \text{range } 0.75\text{-}0.99, \text{all } p < 0.05$). Similar
406 observations were obtained when examining the correlation between eye-target and cursor-
407 target lag at the group level ($R = 0.95, p < 0.001$), or individual level ($R = 0.92 \pm 0.06; \text{range}$
408 $0.74\text{-}0.99, \text{all } p < 0.05$).

409 Next, we compared eye-hand relationship in the EH condition with the one that would
410 have emerged from the adjunction of eye and hand tracking when being performed in
411 isolation (E+H condition). Specifically, we seek to determine whether some form of attraction
412 across effectors would make the eye-cursor distance and lag smaller in EH compared to E+H.
413 As shown by Figure 9, this scheme was largely validated. Two-way ANOVA with
414 CONDITION (EH vs. E+H) and FREQUENCY provided rather similar results for eye-cursor

415 distance and lag. In both cases we found an effect of FREQUENCY ($F(7,189) > 74.43$, $p <$
416 0.001) and CONDITION ($F(1,27) > 84.01$, $p < 0.001$), the latter indicating that the eye-cursor
417 distance and lag were respectively 0.66 cm and 33 ms smaller when both effectors
418 simultaneously tracked the target. FREQUENCY by CONDITION interactions were observed
419 ($F(7,189) > 5.81$, $p < 0.001$), with post-hoc indicating that differences between EH and E+H
420 were all significant but somewhat weaker in the 2.5-3.5 Hz frequency range ($p < 0.05$).

421 Despite drastic changes in hand and eye movements inherent to our manipulation of target
422 refresh rate, those results speak for ubiquitous temporal and spatial coupling between eye and
423 hand actions when these effectors participate conjointly to the tracking task.

424 (Please insert Figure 9 about here)

425 *Additional analyses*

426 Under the H condition, participants were instructed to refrain from eye movements by
427 fixating a central target. To investigate the accuracy of gaze fixation in that condition, we
428 measured the standard deviation (SD) of gaze position along the horizontal and vertical axis
429 for each trial. Averaged across trials, axes, participants and frequencies, this analysis led to an
430 SD of 0.28 cm. For comparison purposes, when gaze was free, that SD was respectively 2.90
431 and 2.75 cm under the E and EH condition. Altogether, this 10-fold difference suggests that
432 participants coped rather well with the instruction to fixate the central cross in the H
433 condition. Next, considering that target eccentricity alters hand tracking performance under
434 eye fixation, we ensured that the mean Euclidian distance between the moving target and the
435 fixation cross was comparable across target frequencies. Averaged across patterns, mean
436 target eccentricity ranged between 5.99 and 6.10 cm depending on the target frequency. We
437 reason that such small differences ($< 2\%$) in target eccentricity were unlikely to account for
438 the drastic changes in hand tracking performance induced by target frequency under the gaze
439 fixed condition (see Figure 8A).

440 Because earlier reports emphasized that saccadic activity was tempered down when
441 continuous manual tracking was performed concurrently with eye tracking (21, 24), we
442 wished to explore whether this finding extended to all our target frequencies. Two-way
443 ANOVA of the saccade rate revealed a main effect of CONDITION ($F(1,27) = 51.19$,
444 $p < 0.001$) such that, averaged across all frequencies, this rate was 11% smaller in EH
445 compared to E. There was also a main effect of FREQUENCY ($F(7,189) = 93.83$, $p < 0.001$)
446 and a FREQUENCY by CONDITION interaction ($F(7,189) = 4.88$, $p < 0.001$). Post-hoc of
447 the interaction revealed significant differences between E and EH at all frequencies except at
448 3 and 3.5 Hz ($p > 0.16$), namely in the vicinity of the transition in hand movement dynamics.

449

450 **DISCUSSION**

451 A first objective of this study was to offer a fair comparison between eye-hand
452 coordination in discrete and continuous movements by using the same setup and participants.
453 A second objective was to explore how eye-hand coordination is organized for actions lying
454 at the frontier of discrete and continuous movements. To achieve these two goals, we relied
455 on a tracking task in which the target visual refresh rate was varied. So far, our results brought
456 the following key findings. First, although a rather abrupt transition between discrete and
457 continuous hand movement was found at about 3 Hz, changes in eye movements appeared
458 more gradual as evidenced by a progressive trade-off between fixations and smooth pursuit
459 episodes. Importantly, despite key changes in eye and hand movements, eye-hand
460 interdependence was omnipresent and persisted all the way from discrete to continuous
461 movements, including those in the vicinity of the transition (albeit sometimes less
462 intensively). This ubiquitous relationship between eye and hand was not only evidenced by
463 mirror changes in their tracking accuracy, but also when contrasting their behaviors during
464 separate and concurrent tracking. We propose now to discuss these findings in more detail,

465 with particular attention to the similarities/differences between eye and hand behavior but also
466 to the possible asymmetries in their coupling.

467

468 *Different transitions in hand and eye movements*

469 The separation between discrete and continuous actions is a pillar of behavioral
470 neuroscience (6). Here by means of manipulating the target refresh rate in a tracking task, we
471 were able to induce substantial changes in hand movement dynamics. As expected, at the
472 lower frequencies hand movements were essentially discrete (as evidenced by numerous
473 pauses with minimal acceleration and velocity), whereas at the highest frequencies hand
474 movements were mostly continuous. Importantly the transition between these two types of
475 movements occurred rather abruptly (i.e. within a few frequency bins, see Figure 6). This
476 finding is reminiscent of other studies that also report a rather abrupt switch between discrete
477 and continuous actions during reciprocal aiming task, no matter whether the frequency of
478 movement was explicitly set by a metronome (6, 49) or emerging from accuracy constraints
479 as in the Fitts task (60–62). The fact that here we report a higher critical frequency (about 3
480 Hz) than in previous studies (typically around 2 Hz) may result from different settings in
481 terms of target motion. In previous studies, participants were required to make reciprocal hand
482 movements between two targets whose position was fixed. The transition from discrete to
483 continuous movements is favored by the fact that merging the deceleration phase in one
484 direction with the acceleration phase in the opposite direction (next movement) is more
485 efficient in terms of muscular energy (61–63). Because in our study the target position
486 changed constantly from one location to a new one, whose coordinates were difficult to
487 anticipate (especially at the lowest refresh rates, see further the section “limitations and
488 delimitations”), the optimization process described above was less likely to contribute, and
489 this may have retarded the transition from discrete to continuous movement.

490 Changes in eye movements were also manifest when modulating the target refresh rate.
491 Although it was largely expected that participants would employ a ‘*fixation-and-saccade*’
492 regime at low frequency as previously reported in discrete pointing tasks (25–30, 34), and a
493 ‘*smooth pursuit-and-saccade*’ regime at high frequency as previously found during tracking
494 tasks (21, 23, 24, 41, 64, 65), it was unclear how the transition would operate between these
495 two regimes. As shown by Figure 7D, the transition in eye movements was more gradual than
496 for hand movements, allowing the coexistence of fixations, saccades, and smooth pursuit for
497 many intermediate frequencies. Those separate dynamics suggest that eye and hand
498 transitions are driven by separate mechanisms. Although hand movements seem to be driven
499 by clear attractors (leading to only discrete or continuous movement), greater flexibility is
500 offered in terms of eye movements. The first part of this proposition resonates with the work
501 of Huys and collaborators (6) suggesting that reciprocal discrete and continuous hand
502 movements are subtended by distinct attractors (respectively ‘fixed point’ and ‘limit cycle’).
503 However, to our knowledge, no similar study has yet investigated the putative nature of
504 attractors driving eye movements. Altogether, despite much evidence of eye-hand
505 interdependence (see the next section), these separate dynamics during the transition implies
506 some flexibility between eye and hand actions.

507 Let us now comment in more details the tradeoff between fixations and smooth pursuit.
508 Considering that access to visual information during saccade is challenging (66–68),
509 participants are presumably left with fixations and smooth pursuit episodes to infer current
510 target and cursor positions. Interestingly, when we add the percentage of time spent in
511 fixation and smooth pursuit, the resulting sum is rather high and does not vary much across
512 target frequencies ($80.0 \pm 2.4\%$). One could reason that despite key changes in task
513 constraints induced by target frequency, the need for visual information to guide the hand
514 remains relatively unchanged. Ultimately, the tradeoff between smooth pursuit and fixations

515 would simply occur to maintain reliable access to cursor and target. Whether this 80% is some
516 kind of gold standard will have to be explored using other tasks. Still, we already know that
517 when tracking was performed with the eyes only, this percentage slightly dropped ($78.0 \pm$
518 2.1%) suggesting that reliance on visual information is a bit weaker when there is no need to
519 guide the hand.

520 At a more general level, there is growing evidence that eye movements (fixations,
521 saccades, and smooth pursuit) rely on partly common pathways that share some inputs, an
522 organization allowing eye movements to work in synergy when a main objective is to keep a
523 target on (or near) the fovea (40, 45–48). Our findings echo with this scheme. Indeed, not
524 only we observed a gradual transition in eye movements with target frequency, but we also
525 noticed, regardless of whether the hand was involved, the ability to swiftly engage fixations,
526 saccades, and smooth pursuit at intermediate frequencies (see examples in the middle row of
527 Figure 5). Although the current results do not provide direct information about the neuronal
528 circuitry underlying each type of eye movement, they speak in favor of an intricate network in
529 which fixations, saccades, and smooth pursuit can be flexibly triggered as a function of task
530 demands.

531

532 *Asymmetrical interdependence between eye and hand tracking performance*

533 Our results clearly showed mutual influence between eye and hand actions. Not only
534 recruiting the hand influenced eye actions, but the presence/absence of eye movements also
535 influenced hand tracking performance (see Figure 8). However, the extent of these effects
536 appears somewhat asymmetrical. Specifically, although recruiting the hand impacted on both
537 the eye-target distance and lag (see Figure 8C and D) for all refresh rates, constraining eye
538 movements did not impact on the cursor-target lag (see Figure 8B) or impacted on cursor-
539 target distance only at the higher refresh rates (see Figure 8A). Taken together these results

540 suggest a stronger influence of the hand on the eye than the other way around. This scheme
541 resonates with other observations reported elsewhere. First, when comparing the timing of eye
542 and hand corrections to abrupt changes in target direction, it was found that recruiting the
543 hand impacted on the latency of the eye, while imposing eye fixation did not impact on the
544 latency of the hand (41). Second, when aiming for two possible targets with eye and hand,
545 preferences for one target are dictated by hand preferences rather than eye preferences (69).
546 Third, it has been shown that the latency of eye movements increases when the initiation of
547 reach is slowed down either by using the non-dominant (left) hand (70), or when visual
548 feedback is reversed (71). Finally, this scheme echoes with recent observations showing that,
549 during reaching, information flow from the parietal reach region (associated with hand
550 discrete movement) to the lateral intraparietal area (associated with saccadic eye movement)
551 is larger than in the opposite direction (11). Taken together, all these studies suggest that, to a
552 large extent, eye movements are yoked to hand motor performance when being directed
553 toward a common goal. The main contribution of our study is to extend this scheme beyond
554 the specific context of reaching (discrete) movements.

555 We now briefly discuss the possible origin of an asymmetrical eye-hand relationship in the
556 context of our study. We propose that this behavior stems from opposite constraints of the
557 visual system on eye and hand tracking. On the one hand, employing rather
558 complex/unpredictable target trajectories makes access to online visual feedback key for
559 tracking performance. In this context, reducing the number of catch-up saccades limits
560 disruptions in visual inflow (72) and thus benefits to hand tracking (21, 24, 73). On the other
561 hand, catch-up saccades are key to reduce ongoing eye tracking error (38). Ultimately, dual
562 tracking (EH) requires mediating eye and hand performance. So far, our results suggest that
563 hand tracking is prioritized at the expense of eye tracking considering that the latter becomes
564 less accurate when the hand is involved. In contrast, eye fixation did not influence much hand

565 tracking at the low and intermediate frequencies, presumably because peripheral vision (up to
566 15°) was sufficient in our task. Eye fixation only began to influence hand movements at the
567 highest frequencies, namely when smooth pursuit should have been normally triggered. As
568 target eccentricity remained constant across frequencies, the detrimental effect of fixation on
569 hand tracking cannot be attributed to a lack of retinal information but rather to the absence of
570 extraretinal information, smooth pursuit being key to predict target motion (74, 75). Even if
571 target motion prediction should normally benefit to both effectors, we reason that hand
572 tracking relies more heavily on this prediction because it does not benefit from fast corrective
573 mechanisms similar to catch-up saccades.

574

575 *Eye-hand coordination is omnipresent*

576 Even though eye and hand exhibited different dynamics with respect to changes in target
577 refresh rate, and rather asymmetrical interdependence in terms of tracking performance, other
578 findings corroborate the fact that eye and hand actions share an intimate relationship. First, we
579 showed that their movement characteristics are not the same when they work conjointly or in
580 isolation. The transition between discrete and continuous hand movements depends on
581 whether the eyes are free to move (see Figure 6), reciprocally the composition of eye
582 movements depends on whether the hand is involved (see Figure 7). Second, we showed that
583 during concurrent eye-hand tracking, eye and hand tracking performances are strongly
584 correlated. Namely when the target rate increased, eye and hand tracking accuracy improved
585 in a very similar way (see Figure 8). Third, for all target frequencies, we observed a tight
586 temporal and spatial bound between gaze and cursor position (see Figure 9). Indeed, both the
587 Euclidean distance and temporal lag between gaze and cursor appeared smaller than what
588 would have been expected from these effectors when working in isolation. Altogether these

589 results provide clear evidence that dual tracking cannot be accounted by simple superposition
590 of eye and hand tracking.

591 Although evidence for eye-hand coordination was already provided in the separate context
592 of discrete (27, 28, 34, 76, 77) and continuous hand movements (21, 24, 44, 78, 79), we
593 believe that the merit of our study resides not only in offering a direct comparison between
594 these two contexts, but also in providing evidence that eye-hand coordination persists for
595 movements lying at the frontier between discrete and continuous ones. Still, to be fair, some
596 indices suggest that in the vicinity of the transition, eye-hand coordination may not have been
597 as efficient as it was for conventional (discrete/continuous) movements. Indeed, when target
598 frequency was around 3 Hz, we found that the temporal and spatial coupling between gaze
599 and cursor was somewhat weaker (see Figure 9). Moreover, in contrast to high and low target
600 frequencies, including or not the hand did not impact on saccadic activity at the intermediate
601 frequencies (3 and 3.5 Hz). These features are reminiscent of one of our study in which
602 behavioral transitions were associated with destabilization in sensorimotor processes (50).

603

604 *Limitations and delimitations*

605 First, we would like to stress that the simultaneous sorting of saccades, fixations, and
606 smooth pursuit episodes using the same algorithm for all the participants, under all
607 experimental conditions, was a challenging endeavor, even when assisted by visual inspection
608 of the signals. Although this challenge is acknowledged in the literature (80, 81), especially
609 when pursuit speed is low (82), there is not yet a consensus on how this sorting should be
610 performed. For the current dataset, teasing apart fixations from slow smooth pursuit episodes
611 was most challenging. As a result, the residual activities found in smooth pursuit under
612 discrete target jumps (about 5% at 1.5 Hz), or in fixation under continuous target motion
613 (about 4% at 240 Hz) need to be considered cautiously (see Figure 7). Although future

614 progress in the segmentation of eye movements will be helpful to assess the relevance of these
615 residuals, all our pilot analyses for categorizing eye movements confirmed the presence of a
616 gradual shift from fixation to smooth pursuit as the target rate increased.

617 Second, it is unclear to what extent the current findings obtained by means of small
618 hand movements with a joystick would apply to a more natural context in which participants
619 would have to directly track the target with their finger using whole arm movements (83).
620 Although we did not formally repeat our protocol in these conditions, comparisons with
621 previous studies suggest that some of our findings can transcend changes in task settings.
622 Indeed, in one of our seminal studies (21) participants had to perform planar movements of
623 the arm while tracking with their fingertip rather similar target trajectories, and a similar
624 finding was that saccadic activity was reduced under concurrent eye hand tracking compared
625 to eye alone tracking (an effect reported by other labs when controlling a cursor by means of a
626 mouse (24) or via isometric contractions (42)). Regarding the occurrence of an abrupt
627 transition between discrete and continuous movements when manipulating the joystick, as
628 exposed previously, a similar finding has been reported when participants employ whole arm
629 movements (49), or index finger movements (6). However, eye recordings were not
630 performed in these studies leaving open the nature of transitions in eye movements.

631 A third issue relates to the possible impact of target motion unpredictability on our
632 findings. When designing our study, employing comparable target trajectories was an initial
633 concern to fairly compare discrete and continuous tracking movements. However, one side
634 effect of discretizing our pseudorandom but continuous trajectories (i.e. combinations of
635 sinusoids) was to increase their unpredictable nature. Indeed, as the target refresh rate is
636 lowered, the ability to infer the upcoming target position from the previous ones becomes
637 more and more difficult (see Figure 2). Considering the key role of target motion

638 predictability in tracking (84–86), the lower performance of eye and hand under the lower
639 target rates should be considered with caution (see Figure 8).

640 Finally, we would like to point out that our distinction between discrete and
641 continuous actions, although well suited to tease apart reaching and tracking tasks, does not
642 acknowledge manual interception tasks which also provided tremendous amount of
643 information on eye-hand coordination (for reviews see 1, 87, 88). Because a typical
644 interception task relies on the release of fast and brief hand movements in which success is
645 directed at the end of action, it is tempting to consider these as discrete movements. However,
646 additional features of interceptive movements also need to be considered. First, in comparison
647 to conventional reaching, interceptive actions place higher demands on continuous monitoring
648 hand/cursor and target location (88, 89). Second, depending on the context, interceptive
649 actions can rely either on fixations (for instance when using a predefined interception
650 location, see (90)), or on a combination of smooth pursuit and catch-up saccades (91–93).
651 Ultimately, all these features speak for the singularities of interceptive actions with respect to
652 the discrete/continuous movements tested here. Despite these differences, we fully embrace
653 the possibility that progressive changes in certain task parameters during an interception task
654 could similarly lead to a gradual shift between fixations and smooth pursuit.

655

656 **CONCLUSIONS**

657 The main goal of our study was to investigate the resilience of eye-hand coordination
658 across a wide variety of hand movements, including discrete, continuous, and intermediates
659 ones. On the one hand, our results showed that the manipulation of target refresh rate
660 impacted differently hand and eye movements. Namely although hand movements made a
661 rather abrupt transition between a discrete and a continuous regime, eye movements changed
662 more gradually as evidenced by a slow tradeoff between fixations and smooth pursuit

663 episodes. On the other hand, we found, for virtually all target frequencies, evidence of a
664 mutual coupling between these two effectors arguing for shared neural mechanisms.
665 Altogether, our results suggest that eye-hand coordination during visuomotor tracking is
666 ubiquitous, yet flexible enough to allow separate dynamics for each effector. This proposition
667 resonates with recent work showing that, although omnipresent, the temporal coupling
668 between eye and hand actions is sufficiently adjustable to accommodate changes in task
669 constraints (29, 94–96). More generally this work further reinforces the view of an intricate
670 relationship between eye and hand neural systems (10, 97, 98), as well as the notion of
671 synergies across eye movement types (40, 45–48).

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683

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685 No conflicts of interest, financial or otherwise, are declared by the authors.

686

687 **Contributions**

688 AC collected, analysed the data, and draw figures. AC and FD conceived the experiment and
689 drafted the manuscript.

690

691 **Data Availability**

692 Data and code supporting the results reported in the article can be found in the OSF data
693 repository, https://osf.io/s67g5/?view_only=5450f2fc3ed5407b80546214ec3772b5.

694

695 **BIBLIOGRAPHY**

- 696 1. **de Brouwer AJ, Flanagan JR, Spering M.** Functional use of eye movements for an acting system.
697 *Trends in Cognitive Sciences* 25: 252–263, 2021.
- 698 2. **Crawford JD, Medendorp WP, Marotta JJ.** Spatial transformations for eye-hand coordination. *J*
699 *Neurophysiol* 92: 10–19, 2004. doi: 10.1152/jn.00117.2004.
- 700 3. **Land MF, Hayhoe M.** In what ways do eye movements contribute to everyday activities? *Vision*
701 *research* 41: 3559–3565, 2001.
- 702 4. **Hogan N, Sternad D.** On rhythmic and discrete movements: reflections, definitions and
703 implications for motor control. *Experimental brain research* 181: 13–30, 2007.
- 704 5. **Hogan N, Sternad D.** Dynamic primitives of motor behavior. *Biological cybernetics* 106: 727–
705 739, 2012.
- 706 6. **Huys R, Studenka BE, Rheaume NL, Zelaznik HN, Jirsa VK.** Distinct timing mechanisms produce
707 discrete and continuous movements. *PLoS computational biology* 4: e1000061, 2008.
- 708 7. **Schaal S, Sternad D, Osu R, Kawato M.** Rhythmic arm movement is not discrete. *Nature*
709 *neuroscience* 7: 1136–1143, 2004.
- 710 8. **Coudiere A, Fernandez E, de Rugy A, Danion FR.** Asymmetrical transfer of adaptation between
711 reaching and tracking: implications for feedforward and feedback processes. *Journal of*
712 *Neurophysiology* 128: 480–493, 2022. doi: 10.1152/jn.00547.2021.
- 713 9. **Yang CS, Cowan NJ, Haith AM.** De novo learning versus adaptation of continuous control in a
714 manual tracking task. *eLife* 10: e62578, 2021. doi: 10.7554/eLife.62578.
- 715 10. **Hwang EJ, Hauschild M, Wilke M, Andersen RA.** Spatial and temporal eye-hand coordination
716 relies on the parietal reach region. *J Neurosci* 34: 12884–12892, 2014. doi:
717 10.1523/JNEUROSCI.3719-13.2014.
- 718 11. **Kang JU, Mooshagian E, Snyder LH.** Inferring functional organization of posterior parietal
719 cortex circuitry based on information flow. *bioRxiv*: 2023.03. 08.531516, 2023.
- 720 12. **Dean HL, Hagan MA, Pesaran B.** Only coherent spiking in posterior parietal cortex coordinates
721 looking and reaching. *Neuron* 73: 829–841, 2012.
- 722 13. **Mascaro M, Battaglia-Mayer A, Nasi L, Amit DJ, Caminiti R.** The eye and the hand: neural
723 mechanisms and network models for oculomanual coordination in parietal cortex. *Cerebral*
724 *Cortex* 13: 1276–1286, 2003.
- 725 14. **Miall RC, Weir DJ, Stein JF.** Visuo-motor tracking during reversible inactivation of the
726 cerebellum. *Exp Brain Res* 65, 1987. doi: 10.1007/BF00236319.
- 727 15. **Miall RC, Reckess GZ, Imamizu H.** The cerebellum coordinates eye and hand tracking
728 movements. *Nature neuroscience* 4: 638–644, 2001.
- 729 16. **Vercher J-L, Gauthier GM.** Cerebellar involvement in the coordination control of the oculo-
730 manual tracking system: effects of cerebellar dentate nucleus lesion. *Exp Brain Res* 73: 155–
731 166, 1988. doi: 10.1007/BF00279669.

- 732 17. **Biguer B, Jeannerod M, Prablanc C.** The coordination of eye, head, and arm movements during
733 reaching at a single visual target. *Exp Brain Res* 46: 301–304, 1982. doi: 10.1007/BF00237188.
- 734 18. **Bekkering H, Adam JosJ, Kingma H, Huson A, Whiting HTA.** Reaction time latencies of eye and
735 hand movements in single- and dual-task conditions. *Exp Brain Res* 97, 1994. doi:
736 10.1007/BF00241541.
- 737 19. **Johansson RS, Westling G, Bäckström A, Flanagan JR.** Eye–hand coordination in object
738 manipulation. *Journal of neuroscience* 21: 6917–6932, 2001.
- 739 20. **Frens MA, Erkelens CJ.** Coordination of hand movements and saccades: evidence for a common
740 and a separate pathway. *Exp Brain Res* 85, 1991. doi: 10.1007/BF00231754.
- 741 21. **Danion FR, Flanagan JR.** Different gaze strategies during eye versus hand tracking of a moving
742 target. *Scientific reports* 8: 1–9, 2018.
- 743 22. **Gouirand N, Mathew J, Brenner E, Danion FR.** Eye movements do not play an important role in
744 the adaptation of hand tracking to a visuomotor rotation. *Journal of neurophysiology* 121:
745 1967–1976, 2019.
- 746 23. **Koken PW, Erkelens CJ.** Influences of hand movements on eye movements in tracking tasks in
747 man. *Experimental Brain Research* 88: 657–664, 1992.
- 748 24. **Niehorster DC, Siu WW, Li L.** Manual tracking enhances smooth pursuit eye movements.
749 *Journal of vision* 15: 11–11, 2015.
- 750 25. **Abrams RA, Meyer DE, Kornblum S.** Eye-hand coordination: oculomotor control in rapid aimed
751 limb movements. *Journal of experimental psychology: human perception and performance* 16:
752 248, 1990.
- 753 26. **Prablanc C, Echallier JF, Komilis E, Jeannerod M.** Optimal response of eye and hand motor
754 systems in pointing at a visual target. I. Spatio-temporal characteristics of eye and hand
755 movements and their relationships when varying the amount of visual information. *Biol Cybern*
756 35: 113–124, 1979.
- 757 27. **Bekkering H, Adam JJ, van den Aarsen A, Kingma H, Whiting HTA.** Interference between
758 saccadic eye and goal-directed hand movements. *Experimental brain research* 106: 475–484,
759 1995.
- 760 28. **Gribble PL, Everling S, Ford K, Mattar A.** Hand-eye coordination for rapid pointing movements.
761 *Experimental brain research* 145: 372–382, 2002.
- 762 29. **Sailer U, Eggert T, Ditterich J, Straube A.** Spatial and temporal aspects of eye-hand
763 coordination across different tasks. *Experimental Brain Research* 134: 163–173, 2000.
- 764 30. **Neggers SF, Bekkering H.** Ocular gaze is anchored to the target of an ongoing pointing
765 movement. *Journal of Neurophysiology* 83: 639–651, 2000.
- 766 31. **Neggers SF, Bekkering H.** Gaze anchoring to a pointing target is present during the entire
767 pointing movement and is driven by a non-visual signal. *Journal of neurophysiology* 86: 961–
768 970, 2001.

- 769 32. **Prablanc C, Pélisson D, Goodale MA.** Visual control of reaching movements without vision of
770 the limb. I. Role of retinal feedback of target position in guiding the hand. *Exp Brain Res* 62:
771 293–302, 1986.
- 772 33. **Prablanc C, Desmurget M, Gréa H.** Neural control of on-line guidance of hand reaching
773 movements. *Prog Brain Res* 142: 155–170, 2003. doi: 10.1016/S0079-6123(03)42012-8.
- 774 34. **Bekkering H, Sailer U.** Commentary: coordination of eye and hand in time and space. *Progress*
775 *in brain research* 140: 365–373, 2002.
- 776 35. **Helsen WF, Elliott D, Starkes JL, Ricker KL.** Coupling of eye, finger, elbow, and shoulder
777 movements during manual aiming. *Journal of motor behavior* 32: 241–248, 2000.
- 778 36. **Paillard J.** Fast and slow feedback loops for the visual correction of spatial errors in a pointing
779 task: a reappraisal. *Can J Physiol Pharmacol* 74: 401–417, 1996.
- 780 37. **Starkes J, Helsen W, Elliott D.** A menage a trois: the eye, the hand and on-line processing.
781 *Journal of sports sciences* 20: 217–224, 2002.
- 782 38. **Goettker A, Gegenfurtner KR.** A change in perspective: The interaction of saccadic and pursuit
783 eye movements in oculomotor control and perception. *Vision Research* 188: 283–296, 2021.
- 784 39. **Lisberger SG.** Visual guidance of smooth-pursuit eye movements: sensation, action, and what
785 happens in between. *Neuron* 66: 477–491, 2010.
- 786 40. **Orban De Xivry J, Lefèvre P.** Saccades and pursuit: two outcomes of a single sensorimotor
787 process. *The Journal of Physiology* 584: 11–23, 2007. doi: 10.1113/jphysiol.2007.139881.
- 788 41. **Engel KC, Soechting JF.** Interactions between ocular motor and manual responses during two-
789 dimensional tracking. *Prog Brain Res* 142: 141–153, 2003. doi: 10.1016/S0079-6123(03)42011-
790 6.
- 791 42. **Huang C-T, Hwang I-S.** Eye-hand synergy and intermittent behaviors during target-directed
792 tracking with visual and non-visual information. *PLoS ONE* 7: e51417, 2012. doi:
793 10.1371/journal.pone.0051417.
- 794 43. **Xia R, Barnes G.** Oculomanual coordination in tracking of pseudorandom target motion stimuli.
795 *Journal of motor behavior* 31: 21–38, 1999.
- 796 44. **Danion FR, Mathew J, Gouirand N, Brenner E.** More precise tracking of horizontal than vertical
797 target motion with both the eyes and hand. *Cortex* 134: 30–42, 2021. doi:
798 10.1016/j.cortex.2020.10.001.
- 799 45. **Krauzlis RJ, Goffart L, Hafed ZM.** Neuronal control of fixation and fixational eye movements.
800 *Phil Trans R Soc B* 372: 20160205, 2017. doi: 10.1098/rstb.2016.0205.
- 801 46. **Goettker A, Brenner E, Gegenfurtner KR, de la Malla C.** Corrective saccades influence velocity
802 judgments and interception. *Scientific Reports* 9: 5395, 2019.
- 803 47. **Krauzlis RJ, Miles FA.** Release of fixation for pursuit and saccades in humans: evidence for
804 shared inputs acting on different neural substrates. *Journal of Neurophysiology* 76: 2822–2833,
805 1996. doi: 10.1152/jn.1996.76.5.2822.

- 806 48. **Krauzlis RJ.** Recasting the Smooth Pursuit Eye Movement System. *Journal of Neurophysiology*
807 91: 591–603, 2004. doi: 10.1152/jn.00801.2003.
- 808 49. **Sternad D, Marino H, Charles SK, Duarte M, Dipietro L, Hogan N.** Transitions between discrete
809 and rhythmic primitives in a unimanual task. *Frontiers in computational neuroscience* 7: 90,
810 2013.
- 811 50. **Danion F, Jirsa VK.** Motor prediction at the edge of instability: Alteration of grip force control
812 during changes in bimanual coordination. *Journal of Experimental Psychology: Human*
813 *Perception and Performance* 36: 1684, 2010.
- 814 51. **Diedrich FJ, Warren Jr WH.** Why change gaits? Dynamics of the walk-run transition. *Journal of*
815 *Experimental Psychology: Human Perception and Performance* 21: 183, 1995.
- 816 52. **Coudiere A, De Rugy A, Danion FR.** Right-left hand asymmetry in manual tracking: when poorer
817 control is associated with better adaptation and interlimb transfer. *Psychological Research: 1-*
818 *13*, 202.
- 819 53. **Mathew J, Sarlegna FR, Bernier P-M, Danion FR.** Handedness matters for motor control but not
820 for prediction. *Eneuro* 6, 2019.
- 821 54. **Bernier P-M, Mathew J, Danion FR.** Composition and decomposition of visuomotor maps
822 during manual tracking. *Journal of Neurophysiology* 126: 1685–1697, 2021.
- 823 55. **Oldfield RC.** The assessment and analysis of handedness: the Edinburgh inventory.
824 *Neuropsychologia* 9: 97–113, 1971.
- 825 56. **Mathew J, Bernier P-M, Danion FR.** Asymmetrical relationship between prediction and control
826 during visuomotor adaptation. *Eneuro* 5, 2018.
- 827 57. **Blignaut P.** Fixation identification: The optimum threshold for a dispersion algorithm. *Attention,*
828 *Perception, & Psychophysics* 71: 881–895, 2009.
- 829 58. **Salvucci DD, Goldberg JH.** Identifying fixations and saccades in eye-tracking protocols. In:
830 *Proceedings of the 2000 symposium on Eye tracking research & applications*. 2000, p. 71–78.
- 831 59. **Urruty T, Lew S, Ihadaddene N, Simovici DA.** Detecting eye fixations by projection clustering.
832 *ACM Transactions on Multimedia Computing, Communications, and Applications (TOMM)* 3: 1–
833 20, 2007.
- 834 60. **Buchanan JJ, Park J-H, Shea CH.** Target width scaling in a repetitive aiming task: switching
835 between cyclical and discrete units of action. *Experimental Brain Research* 175: 710–725, 2006.
- 836 61. **Lazzari S, Mottet D, Vercher J-L.** Eye-hand coordination in rhythmical pointing. *Journal of motor*
837 *behavior* 41: 294–304, 2009.
- 838 62. **de Vries S, Huys R, Zanone PG.** Keeping your eye on the target: eye–hand coordination in a
839 repetitive Fitts’ task. *Exp Brain Res* 236: 3181–3190, 2018. doi: 10.1007/s00221-018-5369-1.
- 840 63. **Guiard Y.** On Fitts’s and Hooke’s laws: Simple harmonic movement in upper-limb cyclical
841 aiming. *Acta psychologica* 82: 139–159, 1993.

- 842 64. **Gauthier GM, Vercher J-L, Mussa Ivaldi F, Marchetti E.** Oculo-manual tracking of visual targets:
843 control learning, coordination control and coordination model. *Experimental Brain Research* 73:
844 127–137, 1988.
- 845 65. **Steinbach MJ, Held R.** Eye tracking of observer-generated target movements. *Science* 161: 187–
846 188, 1968.
- 847 66. **Goodale MA, Pelisson D, Prablanc C.** Large adjustments in visually guided reaching do not
848 depend on vision of the hand or perception of target displacement. *Nature* 320: 748–750, 1986.
849 doi: 10.1038/320748a0.
- 850 67. **Matin E.** Saccadic suppression: a review and an analysis. *Psychological bulletin* 81: 899, 1974.
- 851 68. **Prablanc C, Martin O.** Automatic control during hand reaching at undetected two-dimensional
852 target displacements. *Journal of Neurophysiology* 67: 455–469, 1992. doi:
853 10.1152/jn.1992.67.2.455.
- 854 69. **Horstmann A, Hoffmann K-P.** Target selection in eye–hand coordination: Do we reach to where
855 we look or do we look to where we reach? *Exp Brain Res* 167: 187–195, 2005. doi:
856 10.1007/s00221-005-0038-6.
- 857 70. **Fisk JD, Goodale MA.** The organization of eye and limb movements during unrestricted
858 reaching to targets in contralateral and ipsilateral visual space. *Experimental brain research* 60:
859 159–178, 1985.
- 860 71. **Armstrong IT, Judson M, Munoz DP, Johansson RS, Flanagan JR.** Waiting for a hand: saccadic
861 reaction time increases in proportion to hand reaction time when reaching under a visuomotor
862 reversal. *Frontiers in Human Neuroscience* 7: 319, 2013.
- 863 72. **Thiele A, Henning P, Kubischik M, Hoffmann K-P.** Neural mechanisms of saccadic suppression.
864 *Science* 295: 2460–2462, 2002.
- 865 73. **Mather JA, Putschat C.** Parallel ocular and manual tracking responses to a continuously moving
866 visual target. *J Mot Behav* 15: 29–38, 1983.
- 867 74. **Brenner E, Smeets JB.** Continuously updating one’s predictions underlies successful
868 interception. *Journal of neurophysiology* 120: 3257–3274, 2018.
- 869 75. **Spering M, Schütz AC, Braun DI, Gegenfurtner KR.** Keep your eyes on the ball: smooth pursuit
870 eye movements enhance prediction of visual motion. *Journal of Neurophysiology* 105: 1756–
871 1767, 2011.
- 872 76. **Fischer B, Rogal L.** Eye-hand-coordination in man: a reaction time study. *Biol Cybern* 55: 253–
873 261, 1986.
- 874 77. **Gopal A, Murthy A.** Eye-hand coordination during a double-step task: evidence for a common
875 stochastic accumulator. *J Neurophysiol* 114: 1438–1454, 2015. doi: 10.1152/jn.00276.2015.
- 876 78. **Engel KC, Anderson JH, Soechting JF.** Similarity in the response of smooth pursuit and manual
877 tracking to a change in the direction of target motion. *Journal of Neurophysiology* 84: 1149–
878 1156, 2000.

- 879 79. **Reina GA, Schwartz AB.** Eye–hand coupling during closed-loop drawing: Evidence of shared
880 motor planning? *Human movement science* 22: 137–152, 2003.
- 881 80. **Komogortsev OV, Karpov A.** Automated classification and scoring of smooth pursuit eye
882 movements in the presence of fixations and saccades. *Behav Res* 45: 203–215, 2013. doi:
883 10.3758/s13428-012-0234-9.
- 884 81. **Nyström M, Holmqvist K.** An adaptive algorithm for fixation, saccade, and glissade detection in
885 eyetracking data. *Behavior Research Methods* 42: 188–204, 2010. doi: 10.3758/BRM.42.1.188.
- 886 82. **Startsev M, Agtzidis I, Dorr M.** 1D CNN with BLSTM for automated classification of fixations,
887 saccades, and smooth pursuits. *Behav Res* 51: 556–572, 2019. doi: 10.3758/s13428-018-1144-2.
- 888 83. **Bertrand JK, Chapman CS.** Dynamics of eye–hand coordination are flexibly preserved in eye-
889 cursor coordination during an online, digital, object interaction task. In: *Proceedings of the 2023*
890 *CHI Conference on Human Factors in Computing Systems*. CHI '23: CHI Conference on Human
891 Factors in Computing Systems. ACM, p. 1–13.
- 892 84. **Lam S-Y, Zénon A.** Information rate in humans during visuomotor tracking. *Entropy* 23: 228,
893 2021.
- 894 85. **Barnes GR.** Cognitive processes involved in smooth pursuit eye movements. *Brain and*
895 *cognition* 68: 309–326, 2008.
- 896 86. **Collewijn H, Tamminga EP.** Human smooth and saccadic eye movements during voluntary
897 pursuit of different target motions on different backgrounds. *The Journal of Physiology* 351:
898 217–250, 1984. doi: 10.1113/jphysiol.1984.sp015242.
- 899 87. **Fiehler K, Brenner E, Spering M.** Prediction in goal-directed action. *Journal of Vision* 19: 10–10,
900 2019.
- 901 88. **Fooker J, Kreyenmeier P, Spering M.** The role of eye movements in manual interception: A
902 mini-review. *Vision Research* 183: 81–90, 2021.
- 903 89. **Brenner E, Smeets JB.** Continuous visual control of interception. *Human movement science* 30:
904 475–494, 2011.
- 905 90. **de la Malla C, Rushton SK, Clark K, Smeets JB, Brenner E.** The predictability of a target's motion
906 influences gaze, head, and hand movements when trying to intercept it. *Journal of*
907 *neurophysiology* 121: 2416–2427, 2019.
- 908 91. **Cámara C, De La Malla C, López-Moliner J, Brenner E.** Eye movements in interception with
909 delayed visual feedback. *Exp Brain Res* 236: 1837–1847, 2018. doi: 10.1007/s00221-018-5257-
910 8.
- 911 92. **Barany DA, Gómez-Granados A, Schroyer M, Cutts SA, Singh T.** Perceptual decisions about
912 object shape bias visuomotor coordination during rapid interception movements. *Journal of*
913 *Neurophysiology* 123: 2235–2248, 2020. doi: 10.1152/jn.00098.2020.
- 914 93. **Fooker J, Spering M.** Eye movements as a readout of sensorimotor decision processes. *Journal*
915 *of Neurophysiology* 123: 1439–1447, 2020. doi: 10.1152/jn.00622.2019.

- 916 94. **Abekawa N, Gomi H, Diedrichsen J.** Gaze control during reaching is flexibly modulated to
917 optimize task outcome. *Journal of Neurophysiology* 126: 816–826, 2021.
- 918 95. **de Brouwer AJ, Spering M.** Eye-hand coordination during online reach corrections is task
919 dependent. *Journal of Neurophysiology* 127: 885–895, 2022. doi: 10.1152/jn.00270.2021.
- 920 96. **Jana S, Gopal A, Murthy A.** Computational mechanisms mediating inhibitory control of
921 coordinated eye-hand movements. *Brain Sciences* 11: 607, 2021.
- 922 97. **Battaglia-Mayer A, Caminiti R.** Chapter 26 - Parieto-frontal networks for eye–hand
923 coordination and movements. In: *Handbook of Clinical Neurology*, edited by Vallar G, Coslett
924 HB. Elsevier, p. 499–524.
- 925 98. **Carey DP.** Eye-hand coordination: eye to hand or hand to eye? *Curr Biol* 10: R416-419, 2000.
- 926

927 **FIGURE CAPTIONS**

928 **Figure 1.** Top view of the experimental setup. Participants sat in front of the screen and
929 controlled the joystick using their right hand. Head movements were restrained with a head
930 rest located at 57 cm from the screen.

931

932 **Figure 2. Discretization of target motion.** In all panels, the thin black dotted line represents
933 the continuous target motion associated either with Trajectory 1 (top row) or Trajectory 2
934 (bottom row). The blue dots represent the successive locations at the which the target is
935 displayed along that trajectory depending on the refresh rate. The arrow indicates the direction
936 of target motion. For clarity, we only display the first 5 seconds (one revolution). In A and D,
937 the refresh rate is set at 2 Hz, in B and E at 4 Hz, and in C and F at 8 Hz. As the refresh rate
938 increases, the number of intermediate target locations increases.

939

940 **Figure 3. Method to tease apart discrete and continuous hand movements.** (A) Typical
941 velocity profile of the hand in the EH condition at 1.5 Hz (only 5s are displayed for clarity).
942 The lower and upper red lines correspond respectively to the 10 and 20cm/s threshold
943 associated with R1 and R2. (B) Corresponding acceleration profile with upper and lower red
944 lines setting threshold values of respectively 100 and -100cm/s². (C) Corresponding heatmaps
945 of velocity-acceleration phase portrait with R1 capturing moments where both cursor velocity
946 and acceleration are low ($0 < \text{vel} < 10$ cm/s, $-100 < \text{acc} < +100$ cm/s²), and R2 capturing moments
947 where cursor acceleration is low, but its velocity is high ($10 < \text{vel} < 20$ cm/s, $-100 < \text{acc} < +100$
948 cm/s²). Panels D, E and F are the corresponding versions of panels A, B and C for a trial at
949 240 Hz performed by the same participant. Visual comparison of panels C and D emphasizes
950 the saliency of R1 and R2 to discriminate the continuous/discrete nature of hand movements.

951

952 **Figure 4. Method to tease apart smooth pursuit and fixation episodes.** (A) The black
953 dotted line represents the 95% confidence ellipse of the eye data (in red) during an
954 undetermined segment. The green and blue arrow correspond respectively to the major and
955 minor axis of the confidence ellipse. Because the ratio between these two axes (12.5) is higher
956 than our threshold value (8), this portion of eye movement is identified as smooth pursuit. (B)
957 Same as A for another undetermined segment. Here the ratio between the major and minor
958 axis of the ellipse is smaller (1.5) than our threshold value, identifying this segment as a
959 fixation.

960

961 **Figure 5. Typical trials under various target refresh rates.** Horizontal gaze and cursor
962 signals in the EH condition by three participants (one per column). The refresh rate is set at
963 1.5 Hz in the top row (A), at 3 Hz in the middle row (B), and at 240 Hz in the bottom row (C).
964 Although each tracking trial was 10s long, only 5s of signals are displayed for clarity. Note
965 the drastic changes in hand movement dynamics and in eye movement types as target refresh
966 rate increases, in particular the coexistence of fixations, saccades, and smooth pursuit at the
967 intermediate target frequency.

968

969 **Figure 6. Heat maps of velocity-acceleration phase portraits as a function of target**
970 **frequency in the EH condition (A) in the H condition (B).** All the data available (4 trials
971 from each subject) are plotted in each insert. Red rectangles represent our 2 regions of interest
972 R1 and R2 intended to capture the discrete vs. continuous nature of hand movements (see
973 methods for more details). In both conditions, note the rather abrupt leftward shift in activity
974 as target frequency increases (albeit earlier in H than in EH).

975

976 **Figure 7. Contribution of fixations, smooth pursuit and saccades to eye movements.** (A)
977 Fraction of time spent in fixation during each trial as a function of target frequency in the EH
978 and E condition. (B) Same as A for smooth pursuit. (C) Same as A for saccades. (D)
979 Respective contribution of each movement type as a function of target refresh rate in the EH
980 condition. (E) Same as D for the E condition. Error bars correspond to SD across subjects.

981
982 **Figure 8. Hand and eye tracking accuracy.** (A) Cursor-target distance as a function of
983 target frequency in condition EH and H. (B) Same as A for cursor-target lag. (C) Eye-target
984 distance as a function of target frequency in condition EH and E. (D) Same as C for eye-target
985 lag. Error bars correspond to SD across subjects. Note the rather similar changes in eye and
986 hand tracking accuracy, and an influence of whether tracking is performed with one or two
987 effectors.

988
989 **Figure 9. Eye-cursor distance (A) and lag (B) as a function of the target refresh rate in**
990 **the EH and E+H condition.** Error bars correspond to SD across subjects.