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How optimal is bimanual tracking? The key role of hand coordination in space

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The authors state they have no conflict of interest.

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JM collected the data. FRD and JM analyzed the data. All authors designed the study and drafted the manuscript.

37 **ABSTRACT**

38 When coordinating two hands to achieve a common goal, the nervous system has to
39 assign responsibility to each hand. Optimal control theory suggests that this problem is solved
40 by minimizing costs such as the variability of movement and effort. However the natural
41 tendency to produce similar movements during bimanual tasks has been somewhat ignored by
42 this approach. Here we consider a task in which participants were asked to track a moving
43 target by means of a single cursor controlled simultaneously by the two hands. Two types of
44 hand-cursor mappings were tested: one in which the cursor position resulted from the average
45 location of two hands (MEAN), and one in which horizontal and vertical positions of the
46 cursor were driven separately by each hand (SPLIT). As expected, unimanual tracking
47 performance was better with the dominant hand than with the more variable non-dominant
48 hand. More interestingly, instead of exploiting this effect by increasing the use of the
49 dominant hand, the contributions from both hands remained symmetrical during bimanual
50 cooperative tasks. Indeed, for both mappings, and even after 6min of practice, the right and
51 left hands remained strongly correlated, performing similar movements in extrinsic space.
52 Persistence of this bimanual coupling demonstrates that participants prefer to maintain similar
53 movements at the expense of unnecessary movements (in the SPLIT task), and of increased
54 noise from the non-dominant hand (in the MEAN task). Altogether, the findings suggest that
55 bimanual tracking exploits hand coordination in space rather than minimizing motor costs
56 associated with variability and effort.

57

58 **NOTEWORTHY**

59 When coordinating two hands to achieve a common goal, optimal control theory
60 proposes that the brain assigns responsibility to each hand by minimizing movement
61 variability and effort. Nevertheless, we show that participants perform bimanual tracking
62 using similar contributions from the dominant and non-dominant hands, despite unnecessary
63 movements and a less accurate non-dominant hand. Our findings suggest that bimanual
64 tracking exploits hand coordination in space rather than minimizing motor costs associated
65 with variability and effort.

66 INTRODUCTION

67 In order to generate simple movements such as reaching or grasping, our body has
68 more degrees of freedom than necessary. How brain solves this redundancy problem is a
69 fundamental issue for the understanding of biological motion (Bernstein 1967, 1996; Guigon
70 et al. 2007; Latash et al. 2001). The computational framework of optimal control theory
71 suggests that when we perform hand movements, muscles and joints are coordinated so as to
72 minimize costs such as effort and/or variability of movement (Harris and Wolpert 1998;
73 Todorov and Jordan 2002; Scott 2004; Todorov 2004; Diedrichsen et al. 2010). Although
74 evidence in favor of this optimization process was originally provided in the context of
75 unimanual movements (Fagg et al. 2002; Harris and Wolpert 1998), the case of bimanual
76 actions has only been recently explored (Córdova Bulens et al. 2018; Diedrichsen 2007;
77 Galna and Sparrow 2006; O’Sullivan et al. 2009; Salimpour and Shadmehr 2014; White and
78 Diedrichsen 2010).

79 Although a wide variety of tasks has been developed to explore the control of
80 bimanual movements (Maes et al. 2017), the optimality of bimanual movement has been
81 investigated using essentially two types of task. In the first task type, participants are asked to
82 control a given force that corresponds to the (vectorial) sum of the force produced by each
83 effector (Córdova Bulens et al. 2018; O’Sullivan et al. 2009; Salimpour and Shadmehr 2014).
84 The results of these isometric studies are consistent with the view that force sharing is
85 assigned with respect to minimization of noise and effort, depending on the context.
86 Salimpour and Shadmehr (2014) reported a greater contribution of the less noisy dominant
87 limb in a multijoint, two-dimensional force-aiming task, whereas O’Sullivan and colleagues
88 (2009) found that effort minimization was more highly weighted than minimization of noise
89 in a unidimensional force matching task. In the other type of task, participants are asked to
90 make reaching movements by moving a cursor presented at the spatial average location of the

91 two hands (Diedrichsen 2007; White and Diedrichsen 2010). Although this protocol elegantly
92 showed that mechanical perturbation of one hand also triggers corrections in the non-
93 perturbed hand (Diedrichsen 2007), it did not address the following two issues. First, we
94 know that one hand is typically more accurate than the other for reaching (Mieschke et al.
95 2001; Roy and Elliott 1986; Schaffer and Sainburg 2017), and this asymmetry in performance
96 has been shown to influence hand assignment (Córdova Bulens et al. 2018; Salimpour and
97 Shadmehr 2014; White and Diedrichsen 2010). Second, Kelso and colleagues established that
98 there is a strong natural coupling between hands when both are being moved simultaneously
99 (Kelso et al. 1979). In particular there is known preference both to activate homologous
100 muscles across limbs (i.e. to move in the same direction in intrinsic muscle space), and to
101 move limbs in the same direction in extrinsic task space (Diedrichsen et al. 2004; Howard et
102 al. 2009; Swinnen et al. 1997, 1998). The goal of this study was to investigate how this bias
103 for moving hands in the same direction in space might influence the putative minimization of
104 effort and variability during a visuomotor tracking task performed with a two-handed cursor.

105 Our motivation for manual tracking lies in the fact that this task, in contrast to
106 reaching a stationary target, requires constant adjustments of ongoing hand motor commands,
107 thereby maximizing the contribution of online control. We reasoned that if optimal control
108 can be considered a plausible, general theory of motor control, it should also account for
109 bimanual visuomotor tracking. Here visuomotor tracking was tested under two types of hand-
110 cursor mapping. In the first mapping (MEAN), we took inspiration from Diedrichsen (2007)
111 so that the cursor position corresponded to the average spatial location of the two hands. In
112 the second mapping (SPLIT), we took inspiration from Neilson and Neilson (2002), and from
113 Swinnen and colleagues (Puttemans et al. 2005; Vangheluwe et al. 2005) so that the vertical
114 and horizontal position of the cursor were controlled separately by the right and left hands.
115 However, a key difference with earlier SPLIT studies was that non-relevant hand movements
116 (i.e. movements that did not contribute to cursor motion) were permitted in our protocol,

117 thereby allowing us to probe the subjects' behavior with respect to this redundant dimension.
118 Finally, for control purposes, unimanual tracking under a conventional mapping was also
119 investigated to characterize the tracking performance and variability associated with the
120 dominant and non-dominant hands.

121 The following hypotheses were formulated. Because tracking a moving target is
122 typically more accurate with the dominant hand (Simon et al. 1952; Carey et al. 2003; Aoki et
123 al. 2016 although see Wilson 1972; Moulton et al. 2017), we reasoned that, if minimizing
124 noise is central, the dominant hand should contribute more to cursor motion during bimanual
125 tracking under the MEAN mapping. In addition, if minimizing effort is critical, we predicted
126 that irrelevant hand movements should be scarce under the SPLIT mapping. Alternatively, if
127 the costs inherent to performing dissimilar hand movements outweigh the motor costs
128 associated with variability and effort, we predicted similar contributions of each hand to
129 cursor motion under the MEAN mapping, as well as a persistence of irrelevant hand
130 movements under the SPLIT mapping. Because learning is an important consideration for the
131 optimization of movement, these predictions were monitored during prolonged practice. As
132 will be shown, our results suggest that the objective of maintaining similar hand movements
133 for the two limbs in extrinsic space drives behavior to a greater extent than that of minimizing
134 noise and effort.

135

136 **MATERIAL AND METHODS**

137 *Participants*

138 Twenty healthy right-handed volunteers (age: 26.8 ± 5.5 , hereinafter mean \pm standard
139 deviation, 12 female) were recruited. Handedness of participants was verified using the
140 Oldfield Handedness Inventory (Oldfield 1971) with a mean group laterality index of 95 ± 12 .
141 All participants gave written consent prior to participation. The experimental paradigm (2016-
142 02-03-007) was approved by the local ethics committee of Aix-Marseille University and

143 complied with the Declaration of Helsinki. Each participant was compensated for his/her
144 participation.

145

146 ***Data Acquisition***

147 Figure 1A shows the experimental set up. Participants were seated comfortably in a
148 dark room facing a screen (BENQ, 1920×1080, 27”inch, 144Hz) positioned on the frontal
149 plane 57 cm away from the participant's eye. Participants' head movements were restrained
150 by a chin rest and a padded forehead rest so that the eyes in primary position were directed
151 toward the center of the screen. In order to block vision of their hands, a mask was positioned
152 under the participants' chin. Depending on the conditions (see later) they were required to
153 hold one or two joysticks (Serie 812, Megatron, France, with ± 25 degrees of inclination
154 along X-Y axes) positioned horizontally on a table in front of the participant. Note that there
155 was no restoring force to bring back the joystick at the central position. Moreover the
156 joysticks were frictionless and used conductive plastic technology allowing quasi-infinite
157 resolution. Both right and left forearms were resting on the table. The output of the joysticks
158 was sent to a multi-channel signal conditioner (MSC12, Entran, Fairfield, NJ), and was
159 sampled at 1000 Hz with a 16 bit resolution.

160 *(insert Figure 1 about here)*

161 ***Experimental Design***

162 During hand tracking (see Figure 1B), participants had to move the joystick(s) with
163 their hand(s) so as to bring a cursor (red disk, 0.5° in diameter) as close as possible to a
164 moving target (blue disk, 0.5° in diameter). The motion of the target resulted from the
165 combination of several sinusoids: two along the frontal axis (one fundamental and a second or
166 third harmonic), and two along the sagittal axis (same procedure). The following equations
167 were used to construct target motion:

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

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

168 This technique was used to generate a pseudo-random 2D pattern while preserving smooth
169 changes in velocity and direction (Danion and Flanagan 2018; Mrotek and Soechting 2007;
170 Soechting et al. 2010). A total of 5 different patterns were used throughout the experiment
171 (see Table 1). The order of patterns was randomized across trials while making sure that each
172 block of trials contained a similar number of each pattern. All trajectories had a period of 5 s
173 (fundamental = 0.2 Hz).

174 *(insert Table 1 around here)*

175 A total of 3 hand-cursor mappings were tested. During unimanual trials, the relation
176 between the joystick motion and its visual consequences on the screen was straightforward,
177 mimicking the behavior of a computer mouse. During bimanual trials, the cursor position was
178 driven by the motion of both joysticks. Two types of mapping could be employed. In the first
179 mapping (MEAN), the XY position of the cursor resulted from the mean position of the right
180 and left joysticks: $X=(X_R+ X_L)/2$ and $Y=(Y_R+ Y_L)/2$ (for a similar procedure see (Diedrichsen
181 2007). In the second mapping (SPLIT), each coordinate of the cursor was driven by a distinct
182 joystick: either $X=X_R$ and $Y=Y_L$ or $X=X_L$ and $Y=Y_R$ (for a similar procedure see (Neilson
183 and Neilson 2002) although here movements of the joysticks along the non-relevant axis were
184 still possible). The gain of the joysticks was similar for all mappings with 25° inclination
185 representing 15 cm (or 15° of visual angle) of cursor displacement on the screen. Each trial
186 had duration of 10s (i.e. two cycles of the same trajectory). Overall each participant
187 performed 65 trials. Each experimental session took no more than 45 minutes.

188 Participants were split in two groups that both successively performed uni- and
189 bimanual trials. The experimental session consisted in 3 phases (see Figure 2). During the
190 initial phase, one group of participants (Group MEAN, N=10) performed first one block of 20

216 To provide further information about adaptation to the SPLIT mapping, we tested
217 another group of 10 right handed participants (age: 26.1 ± 4.2 , laterality index: 91.9 ± 10.5 , 5
218 female) under the same mapping but with different settings of the joysticks. Specifically these
219 participants were asked to perform our bimanual SPLIT tracking task using joysticks that
220 were mechanically restrained to a single axis (1D instead of 2D) by means of rails guiding the
221 handle (for a similar procedure see Neilson and Neilson 2002). Additional measurements
222 indicated that the stiffness of these rails was on the order of 3N/cm, meaning that if a
223 participant applied 3N on the joystick's lever perpendicularly to the rails, the cursor could still
224 move by 1 cm on the screen. Such scaling allows us to quantify the effort produced by the
225 participants along the non-relevant axes. As shown at the bottom of Figure 2, five participants
226 experienced the SPLIT mapping with X-right and Y-left, and the remaining five with the
227 opposite mapping. Each participant completed a total of 60 trials under the same mapping,
228 starting in a block of 40 trials with the guiding rails (fixed joysticks), followed by a block of
229 20 trials in which the rails were removed (free joysticks), allowing hand movements along the
230 irrelevant axis for the task. The main motivation for this design was to investigate whether,
231 after prolonged experience with the restrained joysticks, participants would be more effective
232 at refraining from irrelevant movements when using the unrestrained joysticks. Moreover, for
233 this group, bimanual trials were not preceded by unimanual trials that could possibly prime
234 homologous hand movements in extrinsic space.

235 As will be shown later, we observed that bimanual performance under MEAN could
236 lead to better performance than left hand alone, and performance rather similar to right hand
237 alone (if not better). Because in our previous protocol the bimanual condition was always
238 performed after the two unimanual conditions, we have decided to test another group of 12
239 right handed participants (age: 26.6 ± 4.4 , laterality index: 90.0 ± 10.0 , 5 female) while ruling
240 out any possible bias due to order effects. To achieve this goal, each participant completed 1

241 block of 20 trials successively with the left hand, the right hand, or both (MEAN), but here
242 the order of the 3 blocks was counterbalanced across participants (6 possible orders, 2
243 subjects per order).

244

245 *Data Analysis*

246 To assess hand tracking performance, for each trial we measured the mean Euclidian
247 distance between the cursor and the target. The temporal relationship between cursor and
248 target was estimated by means of cross correlations that simultaneously took into account the
249 vertical and horizontal axes. To simultaneously cross-correlate horizontal (X) and vertical (Y)
250 position signals between effectors, we interleaved the X and Y signals, and always time
251 shifted these interleaved signals by a multiple of two samples (Danion and Flanagan 2018;
252 Flanagan et al. 2008). The time interval eliciting the highest correlation coefficient was kept
253 as an index of the time lag between the signals. Some specific analyses were performed for
254 bimanual tasks. First to evaluate the degree of coupling between the two joysticks, we
255 computed the coefficient of correlation across joysticks, separately for the X and Y axes.
256 Second, to investigate the contribution of each hand we computed the total distance covered
257 by each joystick along the X and Y axes, as well as their associated SD, to provide an
258 estimate of movement amplitude. Finally, to investigate if one hand was leading the other, we
259 calculated the temporal lag between the two joysticks using the cross-correlation technique
260 previously explained. For all of these analyses, the first second of each trial was discarded.

261 To provide an estimate of effort when maneuvering the unrestrained joysticks, we
262 computed the tangential acceleration of the hand (Acc_{tan}) by means of double differentiation
263 of the signals provided by the frictionless joysticks. Averaged across trials and participants,
264 mean absolute Acc_{tan} was on the order of 0.2 m/s^2 . When multiplied by the mass of the hand
265 (about 0.5 kg ; de Leva 1996), this acceleration leads to estimated forces of about 0.1 N .

266

267 *Statistics*

268 Repeated measure ANOVAs were used to assess the possible effects of HAND
269 (right/left), MAPPING (SPLIT/MEAN) and TRIALS (first 3/last 3). The Newman-Keuls
270 technique was used for post-hoc tests in order to correct for multiple comparisons. A
271 logarithmic (z score) transformation was used to normalize the distribution of R values. A
272 0.05 significance threshold was used for all analyses. Because the lack of significant
273 differences across groups is not a validation of the null hypothesis, on a few occasions, we
274 have used Bayesian statistics with the JASP free software (<https://jasp-stats.org>) to quantify
275 how true the null hypothesis was, and report BF₁₀ scores.

276

277 **RESULTS**

278 *Unimanual tasks*

279

280 *(insert Figure 3 about here)*

281 Figure 3 plots two representative trials performed by the same participant when
282 tracking the visual target with the right (dominant) or the left (non-dominant) hand. As
283 expected, manual tracking performance was more accurate when using the right hand.
284 Analyses of mean group cursor-target distance and cursor-target lag presented in Figure 4
285 confirmed this trend. Indeed two-way ANOVA (HAND by GROUP) showed a main effect of
286 HAND ($F(1,18)=53.12$, $p<0.001$), with mean Euclidian distance between cursor and target
287 being 20% greater when using the left hand as compared to using the right hand (2.22 vs. 1.84
288 cm; see Fig. 4A). However this ANOVA showed no significant differences across the two
289 groups of participants ($F(1,18)=0.17$, $p=0.68$, $BF_{10}=0.46$), nor was there a HAND by GROUP
290 interaction ($F(1,18)=1.81$, $p=0.19$). Regarding the temporal relationship between cursor and

291 target (see Fig. 4B), we found that the lag was larger for the left hand than the right hand (90
292 vs. 80 ms; $F(1,18)=6.59$, $p<0.05$), but there was no significant effect of GROUP
293 ($F(1,18)=0.07$, $p=0.80$) nor an interaction ($F(1,18)=0.12$, $p=0.73$). Overall, these analyses
294 confirm an effect of hand dominance (right hand tracking is more accurate), as well as the
295 homogeneity of our groups. The presence of homogeneity facilitates the interpretation of
296 possible group differences as a consequence of manipulations of the hand-cursor mapping
297 during the bimanual trials.

298 *(insert Figure 4 about here)*

299 ***Bimanual MEAN mapping***

300 Assuming that motor noise increases linearly with motor command intensity (Harris
301 and Wolpert 1998), and that, as revealed by our unimanual tasks, motor noise is 1.2 times
302 greater for the left hand than the right hand (as revealed by tracking error), we predicted that
303 the contribution of the right hand should be 1.44 times greater than the contribution of the left
304 hand when the cursor was controlled bimanually under the MEAN mapping. This prediction
305 follows from a minimization of the sum of squared errors (O'Sullivan et al. 2009, equation 2).
306 In contrast to Salimpour and Shadmehr (2014), we did not investigate possible directional
307 effect in the performance of each hand as here the target was constantly changing direction
308 (and velocity).

309 Figure 5 plots one representative bimanual trial under the MEAN mapping. As can be
310 seen, movements of the right and left hands were very similar, with minimal distance between
311 the two joysticks.

312 *(insert Figure 5 about here)*

313 Figure 6 plots the average tracking performance as function of trial rank. For
314 comparison purposes, average unimanual performance is provided on the left side of the
315 graph. Averaged across the 40 trials, tracking performance under the MEAN mapping (1.78

316 cm) was comparable to performance by the right hand alone (1.84 cm; $F(1,9)=1.43$, $p=0.26$;
317 $BF_{10}= 0.61$), and thus smaller than the left hand alone (2.29 cm; $F(1,9)=29.24$, $p<0.001$).
318 Although tracking tended to improve across trials, with cursor-target distance decreasing from
319 1.91 to 1.75 cm between early trials (first three) and late trials (last three), the effect of
320 TRIAL did not reach significance ($F(1,9)=2.60$, $p=0.14$; $BF_{10}= 0.85$). A similar pattern of
321 results was observed when examining the cursor-target lag. Indeed, there was no significant
322 difference between the lag under the MEAN mapping and the lag when using the right hand
323 alone (78 vs. 80 ms; $F(1,9)=0.20$, $p=0.66$, $BF_{10}= 0.41$). However, the lag under the MEAN
324 mapping was marginally smaller than when using the left hand alone (78 vs. 90 ms;
325 $F(1,9)=4.33$, $p=0.06$).

326 *(insert Figure 6 about here)*

327
328 Regarding bimanual coordination, analyses showed that motion of the two joysticks
329 was strongly correlated both in time and in extrinsic space. Indeed, averaged across trials, the
330 correlation coefficient between the joysticks was 0.84 and 0.90 respectively for the X and Y
331 components ($p<0.001$). Analysis of the temporal lag between the two joysticks revealed that
332 neither the right nor the left hand was leading the other, because this lag was not significantly
333 different from 0 ($t(9)=0.63$, $p=0.54$; mean 4.8 ± 7.6 ms). When comparing the total distance
334 covered by each joystick, no significant difference was found between the right and the left
335 hands, either for movements along the X (104.6 vs. 108.9 cm; $F(1,9)=0.56$, $p=0.47$; $BF_{10}=$
336 0.52) or the Y axis (112.1 vs. 110 cm; $F(1,9)=0.11$, $p=0.74$, $BF_{10}= 0.43$). Taken together,
337 these observations are not consistent with a greater involvement of the right hand than the left,
338 as would be predicted if participants were attempting to minimize motor noise.

339 When the MEAN mapping was unexpectedly removed so that only one hand was now
340 in control of the cursor, we observed an overall increase in tracking error. This increase
341 follows from the fact that half of the participants controlled the cursor with the right hand,

342 whereas the other half used the left hand. Indeed mean tracking performance during catch
343 trials (2.03 cm) was not different from the average tracking performance when all unimanual
344 trials involving either right or left hands alone were pooled (2.06 cm). Moreover, despite the
345 fact that only one hand became useful to move the cursor, participants persisted in making
346 similar movements in extrinsic space with both hands. Indeed, the correlation between
347 joysticks was 0.82 and 0.85 respectively for the X and Y components during the catch trials
348 ($p < 0.001$).

349 Because we were intrigued that bimanual performance under MEAN could lead to
350 performance rather similar to right hand alone (if not better), we run a control experiment in
351 which the order of the conditions was counterbalanced. Although this new dataset confirmed
352 that the right hand was more accurate than the left hand (1.59 vs. 1.96 cm; $F(1,11)=36.91$,
353 $p < 0.001$), it appears that the benefit provided by the bimanual condition was smaller than
354 initially observed. Indeed, here bimanual performance (1.67 cm) was somewhat intermediate,
355 meaning that it was better than the left hand alone ($F(1,11)=35.28$, $p < 0.001$), but worse than
356 the right hand alone ($F(1,11)=9.83$, $p < 0.01$). Overall, it appears that bimanual tracking may
357 have benefited from earlier practice under the unimanual conditions in our former experiment.
358

359 *Bimanual SPLIT mapping*

360 Assuming that effort increases with the distance covered by each joystick, and that
361 participants attempt to minimize effort when controlling the cursor bimanually, we predicted
362 that under the SPLIT mapping, hand movements that do not contribute to cursor motion
363 should be scarce, or at least smaller than movements that do contribute to cursor motion.

364 *(insert Figure 7 about here)*

365
366 As can be seen on the typical SPLIT trial displayed in Figure 7, despite the fact that
367 the right hand had no influence over the X cursor position, and that the left hand had no

368 influence over the Y cursor position, both right and left hands performed irrelevant
369 movements along these axes, while remaining strongly coupled. Figure 8 plots the average
370 tracking performance, with unimanual performance on the left side for comparison purposes.
371 Mean SPLIT performance (2.00 cm) was marginally worse than unimanual performance with
372 the right hand (1.85 cm; $F(1,9)=3.92$, $p=0.07$), but better than unimanual performance with
373 the left hand (2.15 cm; $F(1,9)=7.77$, $p<0.05$). Altogether SPLIT performance was equivalent
374 to average performance of pooled unimanual control tasks involving only right hand or left
375 hand movements (2.00 cm). We also noticed a marginal effect of TRIAL ($F(1,39)=1.4$,
376 $p=0.06$), suggesting improvements in tracking performance between early and late trials. A
377 similar pattern of results was observed when examining the cursor-target lag. Indeed we
378 found that the temporal lag under SPLIT (82ms) was comparable to the average lag observed
379 when using the right and left hand in isolation (respectively 78 and 86 ms).

380 Despite the fact that tracking under SPLIT could encourage dissociated hand
381 movements, the motion of the right and left joysticks remained strongly correlated throughout
382 the 40 trials, demonstrating that participants failed to assign a separate contribution to each
383 hand. Indeed, averaged across trials, the mean coefficient correlations between joysticks were
384 0.85 and 0.89 respectively for the X and Y components ($p<0.001$). Regarding the temporal lag
385 between the two joysticks, neither the right nor the left hand led the other; this lag was not
386 significantly different from 0 ($t(9)=1.23$, $p=0.25$; mean 8.5 ± 6.9 ms). Analyses of the total
387 distance covered along the relevant and irrelevant axes showed no significant difference.
388 Indeed, the total distance covered along the X axis was similar whether joystick movement
389 was relevant or not (108.7 vs. 104.7 cm; $F(1,9)=0.97$, $p=0.35$; $BF_{10}=0.61$). A similar
390 observation was made when comparing relevant and irrelevant distances covered along the Y
391 axis (112.6 vs. 110.6 cm; $F(1,9)=0.133$, $p=0.72$ $BF_{10}=0.41$). Overall, participants failed to
392 suppress irrelevant hand movements under SPLIT, and performed the task while maintaining

393 similar hand movements in extrinsic space, an observation that does not support a scheme of
394 effort minimization in this task.

395 When the SPLIT mapping was unexpectedly changed so that right and left hand
396 assignments for X and Y axes were switched, we observed an increase in tracking error. This
397 increase was on the order of 20% when comparing the last 3 SPLIT trials and the first 3 catch
398 trials (1.90 vs. 2.27 cm; $F(1,9)=7.28$; $p<0.05$). Nevertheless this alteration is much smaller
399 than what would have been expected if participants had assigned a separate axis to each hand.
400 Further analyses of the catch trials confirmed that participants persisted in making similar
401 hand movements in extrinsic space, as evidenced by high correlations across joysticks, with
402 0.81 and 0.90 respectively for the X and Y components ($p<0.001$).

403 *(insert Figure 9 about here)*

404
405 To assess whether the production of irrelevant movements would be reduced after
406 prior training with restrained (unidirectional) joysticks, we tested another group of
407 participants (control group). Figure 10A shows the time course of tracking accuracy when
408 these participants used restrained, and then unrestrained joysticks. For comparison purposes,
409 the tracking accuracy of participants who only practiced with the unrestrained joysticks
410 (GROUP SPLIT) was added. As can be seen, the initial tracking performance of the control
411 group was worse than performance of GROUP SPLIT, thereby suggesting that the task
412 became more difficult under dissociated movements. During the first three trials, the
413 Euclidian distance between cursor and target was respectively 3.22 and 2.19 cm for the
414 control group and GROUP SPLIT, an almost 50% difference ($F(1,18)=6.21$, $p<0.05$).
415 However, following 40 trials of practice, participants of the control group improved their
416 tracking skill such that their performance (last three trials) became closer to GROUP SPLIT
417 participants (2.16 vs. 1.90 cm; $F(1,18)=1.19$, $p=0.29$; $BF_{10}=0.60$). Moreover further
418 improvement was observed when participants switched from restrained to free joysticks.

419 Indeed when comparing the first three and last three trials with the free joysticks, the
420 Euclidian distance decreased from 2.27 to 2.01 ($F(1,9)=6.92$, $p<0.05$). Thanks to those extra
421 20 trials with the free joysticks, tracking performance of the control group became even more
422 similar to GROUP SPLIT (2.01 vs. 1.90; $F(1,18)=0.38$, $p=0.54$ $BF_{10}= 0.46$).

423 *(insert Figure 10 about here)*

424 An important issue is whether extended practice with the restrained joysticks favors
425 the suppression of irrelevant hand movements when subsequently using the free joysticks. In
426 Figure 10B, we present the time course of irrelevant hand movements as measured by the SD
427 of the joysticks along the irrelevant axis. As can be seen, during the session with the
428 restrained joysticks, the SD remained close to 1 cm. Thanks to our estimation of the rail's
429 stiffness, this SD suggests contact forces of about 3N, a value substantially higher than the
430 force typically employed to maneuver the unrestrained joysticks (about 0.1N). As soon as the
431 joysticks were freed, irrelevant hand movements strongly increased, and kept growing with
432 further practice. When comparing the first three and the last three trials with the free joysticks,
433 SD increased from 2.91 to 3.34 cm ($F(1,9)=6.92$, $p<0.05$); for comparison purposes, the SD
434 for relevant (red hollow circles) and irrelevant (red filled circles) movement of GROUP
435 SPLIT were respectively 4.55 and 4.63 cm. Finally a significant negative correlation between
436 Euclidian error and irrelevant SD was found across the 20 trials with the free joysticks ($R=-$
437 0.58 ; $p<0.01$), suggesting that irrelevant hand movements facilitated hand tracking.
438 Altogether, these results show that, despite prolonged practice promoting dissociated hand
439 movements, participants were still unable to suppress irrelevant hand movements when
440 subsequently using unrestrained joysticks. Moreover, the production of irrelevant movements
441 was associated with better tracking performance. Overall the analyses of irrelevant hand
442 movements, both with the restrained and unrestrained joysticks, do not support a
443 minimization of effort in our bimanual task.

444

445 **DISCUSSION**

446 Our main objective was to investigate the combined effects of motor costs associated
447 with variability and effort and the natural coupling between hands when tracking a moving
448 target with a two-handed cursor. Our results illustrate the following key findings in right-hand
449 handed people. First, as expected, we observed an effect of hand dominance such that
450 unimanual tracking with the right hand was 20% more accurate than with the left hand.
451 Second, despite this effect of handedness, when participants performed bimanual tracking
452 under the MEAN mapping, the right and left hands contributed equally to cursor motion and
453 were tightly coupled in time and (extrinsic) space. Third, when performing bimanual tracking
454 under the SPLIT mapping, participants failed to suppress irrelevant hand movements, but
455 rather produced coupled hand movements in extrinsic space. In a control experiment, we
456 showed that prior training enforcing dissociated hand movements (by preventing movements
457 along irrelevant dimensions), was not effective in preventing participants from producing
458 coupled, bimanual hand movements whenever permitted. These results suggest that bimanual
459 tracking exploits a preference for coupled hand movements in space rather than resulting from
460 a minimization of movement variability or effort.

461

462 *Failure to assign separate hand contributions under MEAN*

463 In agreement with earlier studies, we found that unimanual tracking was more accurate
464 with the dominant hand (Simon et al. 1952; Carey et al. 2003; Aoki et al. 2016). Moreover the
465 asymmetry in manual dexterity observed in our study (+20% error in the left hand when
466 compared to the right hand) fits rather well with previous studies investigating the optimality
467 of bimanual behavior using isometric tasks that require either to reach a given force level with
468 the fingers pressing on transducers (+23-35% in O'Sullivan et al. 2009), or to generate a force

469 vector with the arms using handles (+18% for Salimpour and Shadmehr 2014). Assuming that
470 optimal performance is reflected by the minimal sum of squared errors, we predicted that the
471 contribution of the right hand should be 44% greater than the contribution of the left hand, an
472 asymmetry that would be consistent with earlier studies (O'Sullivan et al. 2009; Salimpour
473 and Shadmehr 2014). However our observations failed to support this scheme and participants
474 performed the task with both hands contributing equally to target motion. Moreover,
475 kinematic analyses revealed that hand motions were tightly coupled in time and space, with
476 both hands making similar and synchronous movements in extrinsic space. Overall, our
477 results do not support the view of a greater contribution by the less noisy hand. What can be
478 the reason(s) leading to different effects of handedness in our task and in earlier studies? We
479 see two options that relate to the motoric aspects of the task. First in the studies of O'Sullivan
480 et al. (2009) and Salimpour and Shadmehr (2014), participants had to produce isometric
481 forces with the fingers or the arms, whereas our study required actual movements of the hands
482 to manoeuvre the joysticks. However it remains unclear why minimizing variability would be
483 more critical for isometric than for isotonic tasks. Perhaps the mapping between force and
484 cursor feels more arbitrary (and hand specific) than the mapping between position and cursor.
485 Another difference relates to the continuous/discrete nature of the tasks involved. In the
486 studies of O'Sullivan et al. (2009) and Salimpour and Shadmehr (2014), participants had to
487 produce discrete reaching movements (<1s), which contrast with the longer continuous
488 tracking movements required in our study (10s). It is possible that different involvements of
489 feedforward and/or planning mechanisms, as well as constant online adjustments associated
490 with tracking an unpredictable stimulus, might have limited the expression of optimization
491 processes.

492 *Failure to suppress irrelevant hand movements under SPLIT*

493 To assess whether the minimization of effort was crucial for bimanual coordination,
494 we investigated how participants tracked a target with two joysticks, each one controlling the
495 cursor along a single axis. Based on earlier reports supporting the minimization of effort
496 (O'Sullivan et al. 2009), we predicted that participants would refrain from movements that do
497 not contribute to the cursor motion. However, even after 6min practice, our results contrast
498 markedly with this scheme. Indeed, the amount of movement was similar along relevant and
499 irrelevant axes of the joysticks. More specifically we observed that participants consistently
500 performed movements with both hands that were similar to each other in extrinsic space.
501 Because one may argue that the amount of practice was not sufficient to observe the
502 suppression of hand movements along irrelevant task dimensions, we tested another group of
503 participants that received prior training with dissociated hand movements enforced by
504 mechanical restriction. However, our results show that this procedure was ineffective in the
505 sense that substantial irrelevant movements appeared as soon as the mechanical constraints
506 were released (as illustrated in Figure 10). Moreover, when using the restrained joysticks, the
507 force applied by the participants along the irrelevant axis was approximately 30 times greater
508 than the force employed to move the unrestrained joysticks.

509 Taken together our observations obtained with the SPLIT mapping and free joysticks,
510 as well as during and after practice with the restrained joysticks, suggest that minimizing
511 effort was not a key factor in determining the pattern of bimanual coordination selected by
512 participants. What could be the reason(s) leading to these counter-intuitive observations? One
513 possibility is that the energetic cost of wrist movements associated with manipulating our
514 frictionless joysticks might be marginal, especially when compared to the energetic cost
515 associated with full arm reaching movements (Córdova Bulens et al. 2018; Diedrichsen 2007;
516 Salimpour and Shadmehr 2014). As a result, one could argue that minimization of effort did
517 not operate in our task because there was virtually no effort involved. Although this argument

518 may hold for the persistence of irrelevant movements with free joysticks (force $\approx 0.1\text{N}$), it is
519 less obvious why, when using the restrained joysticks, participants applied much stronger
520 forces for irrelevant movements ($\approx 3\text{N}$) than relevant ones, especially considering that the
521 minimization of effort has been found to operate for comparable finger forces (O'Sullivan et
522 al. 2009). Alternatively, it is possible that, in the absence of hand movements, forces applied
523 against the rails provided somatosensory feedback facilitating bimanual coordination. Future
524 experiments using joysticks with haptic feedback may be helpful in clarifying whether
525 increasing the load associated with the motion of the joysticks promotes the minimization of
526 effort. Finally, as previously proposed for the minimization of variability, it is possible that
527 the minimization of effort was more challenging when constant adjustments of hand
528 movements were required in our bimanual tracking task.

529

530 *On optimality and the natural tendency to coordinate both hands in space*

531 So far our results provide little evidence that effort and variability, two quantities
532 repeatedly reported to be optimized during unimanual as well as bimanual reaching (Emken et
533 al. 2007; Franklin et al. 2008; Gaveau et al. 2013; Mistry et al. 2013; O'Sullivan et al. 2009;
534 Salimpour and Shadmehr 2014), are optimized during bimanual tracking. These results are
535 consistent with some reaching studies showing that subjects maintain suboptimal behavior
536 under altered mechanical contexts, even after prior experience of the optimal solution (Ganesh
537 et al. 2010; Kistemaker et al. 2010). Indeed, despite having learned to perform the task with
538 dissociated hand movements in our SPLIT control condition, unnecessary movements (i.e.
539 along the irrelevant dimension) emerged as soon as the mechanical constraints preventing
540 those movements were released. Instead of optimizing behavior for every set of novel task
541 constraints, the nervous system might therefore take advantage of its existing behavioral
542 repertoire (Loeb 2012; de Rugy et al. 2012). In this context, it is important to note that

543 although performance with restrained joysticks approached performance with unrestrained
544 joysticks, they still did not quite equate. This observation is consistent with an additional cost
545 inherent to the production of dissociated hand movements, and fits well with a brain imaging
546 study showing increased activity for dissociated than for coupled right-left finger movements
547 (Meister et al. 2010). Moreover the correlation found between performance improvement and
548 the amount of irrelevant hand movements upon release of the mechanical constraint reflects a
549 benefit associated with the natural tendency to coordinate hands in space. In the context of
550 rhythmic bimanual movements, natural coordination patterns are known to depend upon a
551 coalition of both intrinsic and extrinsic constraints, whereby coordination that involves
552 synchronous muscle contractions and/or synchronous movements in space is more stable
553 (Salesse et al. 2005). In the context of reaching adaptation, there is also evidence for
554 simultaneous representation of sensorimotor transformation for both hands in intrinsic as well
555 as extrinsic coordinate systems. Indeed, interlimb transfer following sensorimotor adaptation
556 in one limb was immediate and maximized when intrinsic and extrinsic reference frames were
557 aligned for the two limbs (Carroll et al. 2014, 2016). The natural tendency to couple the two
558 hands in space is therefore likely to have constrained our bimanual tracking tasks, such that
559 the benefits of exploiting this natural tendency outweighed the motor costs associated with
560 unnecessary movements along irrelevant dimensions, and the preferential use of the more
561 accurate dominant hand.

562 *Limitation*

563 Here we tested the adequacy of optimal control theory for bimanual tracking on the
564 basis of minimizing the sum of squared errors, using an equation provided by O'Sullivan et al.
565 (2009) in the context of a task in which participants had to press against a one dimensional
566 load cell. As a result one may wonder to what extent this equation applies to our two
567 dimensional tracking task in which motor noise may exhibit different dynamics depending on

568 hand movement direction. Although models can be adjusted to account for directional
569 anisotropies of motor noise when reaching static targets (see equation 8 in Salimpour and
570 Shadmehr, 2014), this is less obvious in our task in which the target was constantly changing
571 direction and speed. Moreover, even if we had conducted a separate experiment to properly
572 assess how tracking performance might vary along each individual direction and speed, it
573 would still remain unclear how this behavior applies to the context where both parameters are
574 constantly changing. Although possible directional asymmetries in hand tracking need to be
575 explored, further data processing in our study already reveals that the right hand advantage is
576 similar along the horizontal and vertical axis, suggesting that the right-left hand asymmetry is
577 rather direction insensitive. Overall the contribution of the current study is clearly not on the
578 modeling aspect, but in making the general point that bimanual tracking involves additional
579 constraints of hand coordination in space rather than the mere minimization of variability and
580 effort.

581

582 *Conclusion*

583 Using a simple model, the current study tested the optimality of bimanual coordination
584 with regard to minimization of effort and variability (O'Sullivan et al. 2009; Salimpour and
585 Shadmehr 2014) in the context of bimanual tracking. The fact that our participants failed to
586 assign different movement contributions to the right and left hand, and were unable to
587 suppress irrelevant hand movements, speak against the minimization of effort and variability.
588 The persistence of similar movements in extrinsic space in both versions of our bimanual task
589 suggests that when tracking a continuously moving target, the cost inherent to the production
590 of dissociated hand movements, and/or the benefits associated with the production of similar
591 hand movements, overrules the minimization of effort and variability.

592

593 **BIBLIOGRAPHY**

- 594 **Aoki T, Rivlis G, Schieber MH.** Handedness and index finger movements performed on a small
595 touchscreen. *J Neurophysiol* 115: 858–867, 2016.
- 596 **Bernstein NA.** *The co-ordination and regulation of movements.* Oxford: Pergamon Press, 1967.
- 597 **Bernstein NA.** *Dexterity and Its Development.* Lawrence Erlbaum Associates Inc, 1996.
- 598 **Carey JR, Comnick KT, Lojovich JM, Lindgren BR.** Left- versus right-hand tracking performance by
599 right-handed boys and girls: examination of performance asymmetry. *Percept Mot Skills* 97: 779–788,
600 2003.
- 601 **Carroll TJ, Poh E, de Rugy A.** New visuomotor maps are immediately available to the opposite limb. *J*
602 *Neurophysiol* 111: 2232–2243, 2014.
- 603 **Carroll TJ, de Rugy A, Howard IS, Ingram JN, Wolpert DM.** Enhanced crosslimb transfer of force-field
604 learning for dynamics that are identical in extrinsic and joint-based coordinates for both limbs. *J*
605 *Neurophysiol* 115: 445–456, 2016.
- 606 **Córdova Bulens D, Crevecoeur F, Thonnard J-L, Lefèvre P.** Optimal use of limb mechanics distributes
607 control during bimanual tasks. *J Neurophysiol* 119: 921–932, 2018.
- 608 **Danion FR, Flanagan JR.** Different gaze strategies during eye versus hand tracking of a moving target.
609 *Sci Rep* 8: 10059, 2018.
- 610 **Diedrichsen J.** Optimal task-dependent changes of bimanual feedback control and adaptation. *Curr*
611 *Biol CB* 17: 1675–1679, 2007.
- 612 **Diedrichsen J, Nambisan R, Kennerley SW, Ivry RB.** Independent on-line control of the two hands
613 during bimanual reaching. *Eur J Neurosci* 19: 1643–1652, 2004.
- 614 **Diedrichsen J, Shadmehr R, Ivry RB.** The coordination of movement: optimal feedback control and
615 beyond. *Trends Cogn Sci* 14: 31–39, 2010.
- 616 **Emken JL, Benitez R, Sideris A, Bobrow JE, Reinkensmeyer DJ.** Motor adaptation as a greedy
617 optimization of error and effort. *J Neurophysiol* 97: 3997–4006, 2007.
- 618 **Fagg AH, Shah A, Barto AG.** A computational model of muscle recruitment for wrist movements. *J*
619 *Neurophysiol* 88: 3348–3358, 2002.
- 620 **Flanagan JR, Terao Y, Johansson RS.** Gaze behavior when reaching to remembered targets. *J*
621 *Neurophysiol* 100: 1533–1543, 2008.
- 622 **Franklin DW, Burdet E, Tee KP, Osu R, Chew C-M, Milner TE, Kawato M.** CNS learns stable, accurate,
623 and efficient movements using a simple algorithm. *J Neurosci Off J Soc Neurosci* 28: 11165–11173,
624 2008.
- 625 **Galna B, Sparrow WA.** Learning to minimize energy costs and maximize mechanical work in a
626 bimanual coordination task. *J Mot Behav* 38: 411–422, 2006.
- 627 **Ganesh G, Haruno M, Kawato M, Burdet E.** Motor memory and local minimization of error and
628 effort, not global optimization, determine motor behavior. *J Neurophysiol* 104: 382–390, 2010.

- 629 **Gaveau J, Berret B, Demougeot L, Fadiga L, Pozzo T, Papaxanthis C.** Energy-related optimal control
630 accounts for gravitational load: comparing shoulder, elbow, and wrist rotations. *J Neurophysiol* 111:
631 4–16, 2013.
- 632 **Guigon E, Baraduc P, Desmurget M.** Computational motor control: redundancy and invariance. *J*
633 *Neurophysiol* 97: 331–347, 2007.
- 634 **Harris CM, Wolpert DM.** Signal-dependent noise determines motor planning. *Nature* 394: 780–784,
635 1998.
- 636 **Howard IS, Ingram JN, Körding KP, Wolpert DM.** Statistics of natural movements are reflected in
637 motor errors. *J Neurophysiol* 102: 1902–1910, 2009.
- 638 **Kelso JA, Southard DL, Goodman D.** On the nature of human interlimb coordination. *Science* 203:
639 1029–1031, 1979.
- 640 **Kistemaker DA, Wong JD, Gribble PL.** The central nervous system does not minimize energy cost in
641 arm movements. *J Neurophysiol* 104: 2985–2994, 2010.
- 642 **Latash ML, Scholz JF, Danion F, Schöner G.** Structure of motor variability in marginally redundant
643 multifinger force production tasks. *Exp Brain Res Exp Hirnforsch Expérimentation Cérébrale* 141: 153–
644 165, 2001.
- 645 **de Leva P.** Adjustments to Zatsiorsky-Seluyanov’s segment inertia parameters. *J Biomech* 29: 1223–
646 1230, 1996.
- 647 **Loeb GE.** Optimal isn’t good enough. *Biol Cybern* 106: 757–765, 2012.
- 648 **Maes C, Gooijers J, Orban de Xivry J-J, Swinnen SP, Boisgontier MP.** Two hands, one brain, and
649 aging. *Neurosci Biobehav Rev* 75: 234–256, 2017.
- 650 **Meister IG, Foltys H, Gallea C, Hallett M.** How the brain handles temporally uncoupled bimanual
651 movements. *Cereb Cortex N Y N 1991* 20: 2996–3004, 2010.
- 652 **Mieschke PE, Elliott D, Helsen WF, Carson RG, Coull JA.** Manual asymmetries in the preparation and
653 control of goal-directed movements. *Brain Cogn* 45: 129–140, 2001.
- 654 **Mistry M, Theodorou E, Schaal S, Kawato M.** Optimal control of reaching includes kinematic
655 constraints. *J Neurophysiol* 110: 1–11, 2013.
- 656 **Moulton E, Galléa C, Kemlin C, Valabregue R, Maier MA, Lindberg P, Rosso C.** Cerebello-Cortical
657 Differences in Effective Connectivity of the Dominant and Non-dominant Hand during a Visuomotor
658 Paradigm of Grip Force Control. *Front Hum Neurosci* 11, 2017.
- 659 **Mrotek LA, Soechting JF.** Target interception: hand-eye coordination and strategies. *J Neurosci* 27:
660 7297–7309, 2007.
- 661 **Neilson PD, Neilson MD.** Anisotropic tracking: evidence for automatic synergy formation in a
662 bimanual task. *Hum Mov Sci* 21: 723–748, 2002.
- 663 **Oldfield RC.** The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*
664 9: 97–113, 1971.

- 665 **O'Sullivan I, Burdet E, Diedrichsen J.** Dissociating variability and effort as determinants of
666 coordination. *PLoS Comput Biol* 5: e1000345, 2009.
- 667 **Puttemans V, Wenderoth N, Swinnen SP.** Changes in Brain Activation during the Acquisition of a
668 Multifrequency Bimanual Coordination Task: From the Cognitive Stage to Advanced Levels of
669 Automaticity. *J Neurosci* 25: 4270–4278, 2005.
- 670 **Roy EA, Elliott D.** Manual asymmetries in visually directed aiming. *Can J Psychol* 40: 109–121, 1986.
- 671 **de Rugy A, Loeb GE, Carroll TJ.** Muscle coordination is habitual rather than optimal. *J Neurosci Off J*
672 *Soc Neurosci* 32: 7384–7391, 2012.
- 673 **Salesse R, Oullier O, Temprado J-J.** Plane of motion mediates the coalition of constraints in rhythmic
674 bimanual coordination. *J Mot Behav* 37: 454–464, 2005.
- 675 **Salimpour Y, Shadmehr R.** Motor costs and the coordination of the two arms. *J Neurosci Off J Soc*
676 *Neurosci* 34: 1806–1818, 2014.
- 677 **Schaffer JE, Sainburg RL.** Interlimb differences in coordination of unsupported reaching movements.
678 *Neuroscience* 350: 54–64, 2017.
- 679 **Scott SH.** Optimal feedback control and the neural basis of volitional motor control. *Nat Rev Neurosci*
680 5: 532–546, 2004.
- 681 **Simon JR, Crow TWD, Lincoln RS, Smith KU.** Effects of Handedness on Tracking Accuracy. *Mot Ski Res*
682 *Exch* 4: 53–57, 1952.
- 683 **Soechting JF, Rao HM, Juveli JZ.** Incorporating prediction in models for two-dimensional smooth
684 pursuit. *PLoS One* 5: e12574, 2010.
- 685 **Swinnen SP, Jardin K, Meulenbroek R, Dounskaia N, Den Brandt MH.** Egocentric and allocentric
686 constraints in the expression of patterns of interlimb coordination. *J Cogn Neurosci* 9: 348–377, 1997.
- 687 **Swinnen SP, Jardin K, Verschueren S, Meulenbroek R, Franz L, Dounskaia N, Walter CB.** Exploring
688 interlimb constraints during bimanual graphic performance: Effects of muscle grouping and direction.
689 *Behav Brain Res* 90: 79–87, 1998.
- 690 **Todorov E.** Optimality principles in sensorimotor control. *Nat Neurosci* 7: 907–915, 2004.
- 691 **Todorov E, Jordan MI.** Optimal feedback control as a theory of motor coordination. *Nat Neurosci* 5:
692 1226–1235, 2002.
- 693 **Vangheluwe S, Wenderoth N, Swinnen SP.** Learning and transfer of an ipsilateral coordination task:
694 evidence for a dual-layer movement representation. *J Cogn Neurosci* 17: 1460–1470, 2005.
- 695 **White O, Diedrichsen J.** Responsibility Assignment in Redundant Systems. *Curr Biol* 20: 1290–1295,
696 2010.
- 697 **Wilson RV.** The Effect of Handedness on a Tracking Task [Online]. Royal Aircraft Establishment
698 Farnborough (UK).<http://www.dtic.mil/docs/citations/AD0753785> [21 Mar. 2018].
- 699

700 **FIGURE CAPTIONS**

701 **Figure 1.** Apparatus and experimental task. A. Top view of a participant sitting in the
702 experimental setup. B. Schematic view of the screen during hand tracking. The target path
703 was not displayed on the screen (see Material and Methods for further information).

704

705 **Figure 2.** Experimental design (see Material and Methods for further information).

706

707 **Figure 3.** Typical hand tracking trials performed by the same participant under the same
708 target trajectory. Left and right columns display cursor and target position when moving the
709 joystick respectively with the left and right hand. Upper and middle rows display respectively
710 the horizontal (X) and vertical (Y) components of hand (cursor) and target motion. Lower row
711 displays the corresponding XY trajectories of cursor and target. Note the greater accuracy of
712 hand tracking when using the right dominant hand.

713

714 **Figure 4.** Comparison between right and left hand performance during unimanual tracking. A.
715 Euclidian distance between cursor and target. B. Temporal lag between cursor and target.
716 Error bars represent the standard error of the mean (SEM). Note how tracking performance is
717 consistently better for both groups when using the right (dominant) hand as compared to the
718 left (non-dominant) hand.

719

720 **Figure 5.** Typical bimanual trial under the MEAN hand-cursor mapping. Left and central
721 graphs display respectively the horizontal(X) and vertical (Y) components of each hand,
722 cursor and target movement. Right graph displays the corresponding XY trajectories of cursor
723 and target. Signals that were not displayed on the screen are represented by dashed lines. Note
724 how similar are right and left hand motions.

725

726 **Figure 6.** Mean tracking performance under the MEAN bimanual condition as a function of
727 trial number. Error bars represent SEM.

728

729 **Figure 7.** Typical bimanual trial under the SPLIT hand-cursor mapping. Left and central
730 graphs display respectively the horizontal (X) and vertical (Y) components of each hand,
731 cursor and target movement. Right graph displays the corresponding XY trajectories of cursor

732 and target. Signals that were not displayed on the screen are represented by dashed lines. Note
733 how similar are the right and left hand motions.

734

735 **Figure 8.** Mean tracking performance under the bimanual SPLIT condition as a function of
736 trial number. Error bars represent SEM.

737

738 **Figure 9.** Typical SPLIT bimanual trials during the control experiment. The left column
739 displays one trial performed when using the restrained joysticks (i.e. that could only move
740 along one axis). The right column displays one follow up trial when the same participant
741 employs the unrestrained joysticks (i.e. free to move in 2D). Upper and lower rows display
742 respectively the horizontal and vertical components of each hand, cursor and target
743 movement. Signals that were not displayed on the screen are represented by dashed lines.
744 Note the presence of irrelevant hand motion when using the unrestrained joysticks.

745

746 **Figure 10.** Comparison between tracking performance with and without the rails on the
747 joysticks. A. Euclidian error as a function of trial number in Group 2 and in the control group.
748 B. Same as A for the SD of hand movements along the irrelevant axis. For comparison
749 purposes, SD of hand movements along the relevant axis are presented as hollow red circles
750 for Group SPLIT. The red dotted lines provide an extension of Group SPLIT computed over
751 the last trial. Note how irrelevant hand movements built up immediately after the removal of
752 the rails in the control group. Error bars represent SEM.

753

754

755 **TABLE**

756

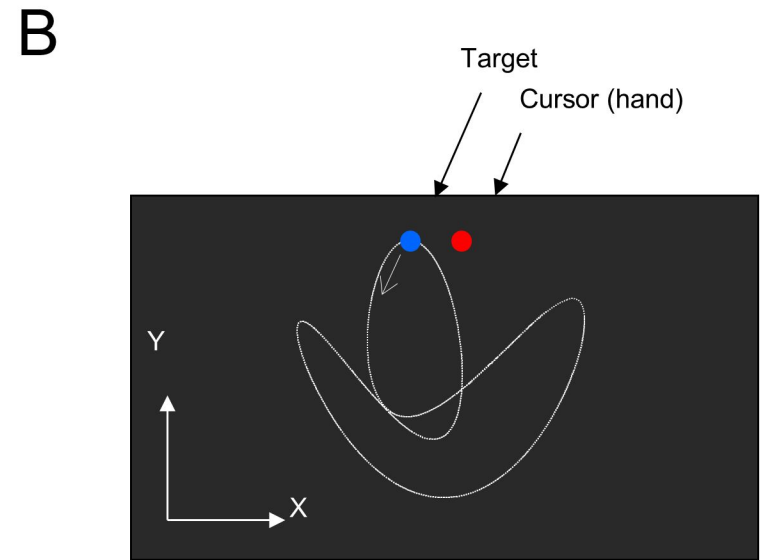
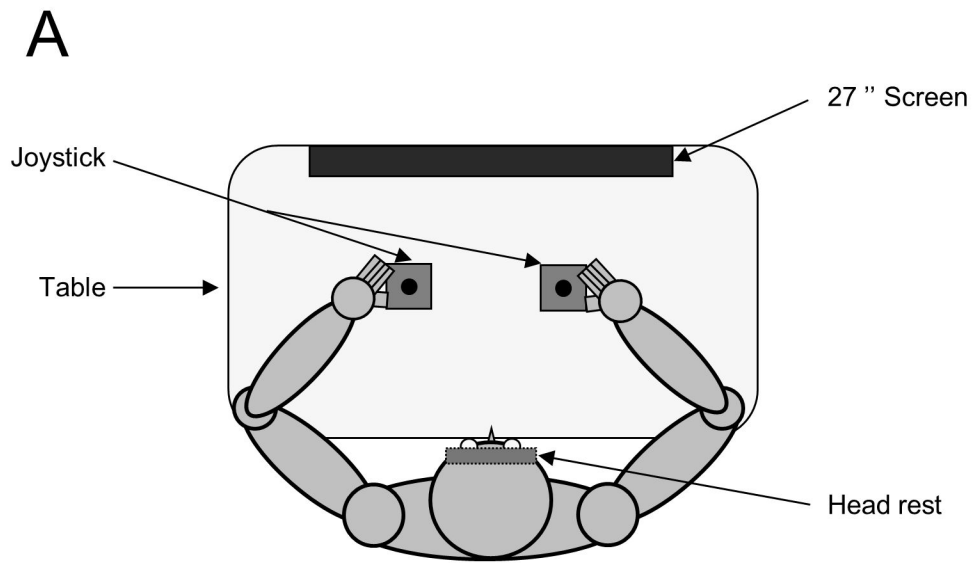
| Trajectory | A1x (cm) | A2x (cm) | Harmonic x | Phase x (°) | A1y (cm) | A2y (cm) | Harmonic y | Phase y (°) |
|------------|----------|----------|------------|-------------|----------|----------|------------|-------------|
| 1 | 5 | 5 | 2 | 45 | 5 | 5 | 3 | -135 |
| 2 | 4 | 5 | 2 | -60 | 3 | 5 | 3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

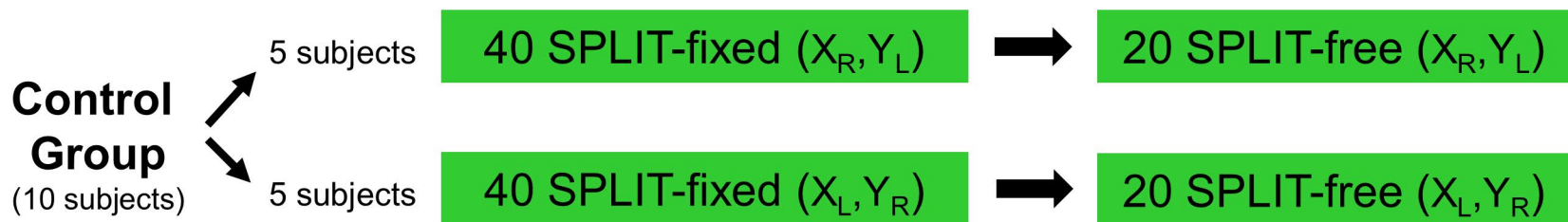
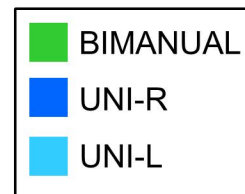
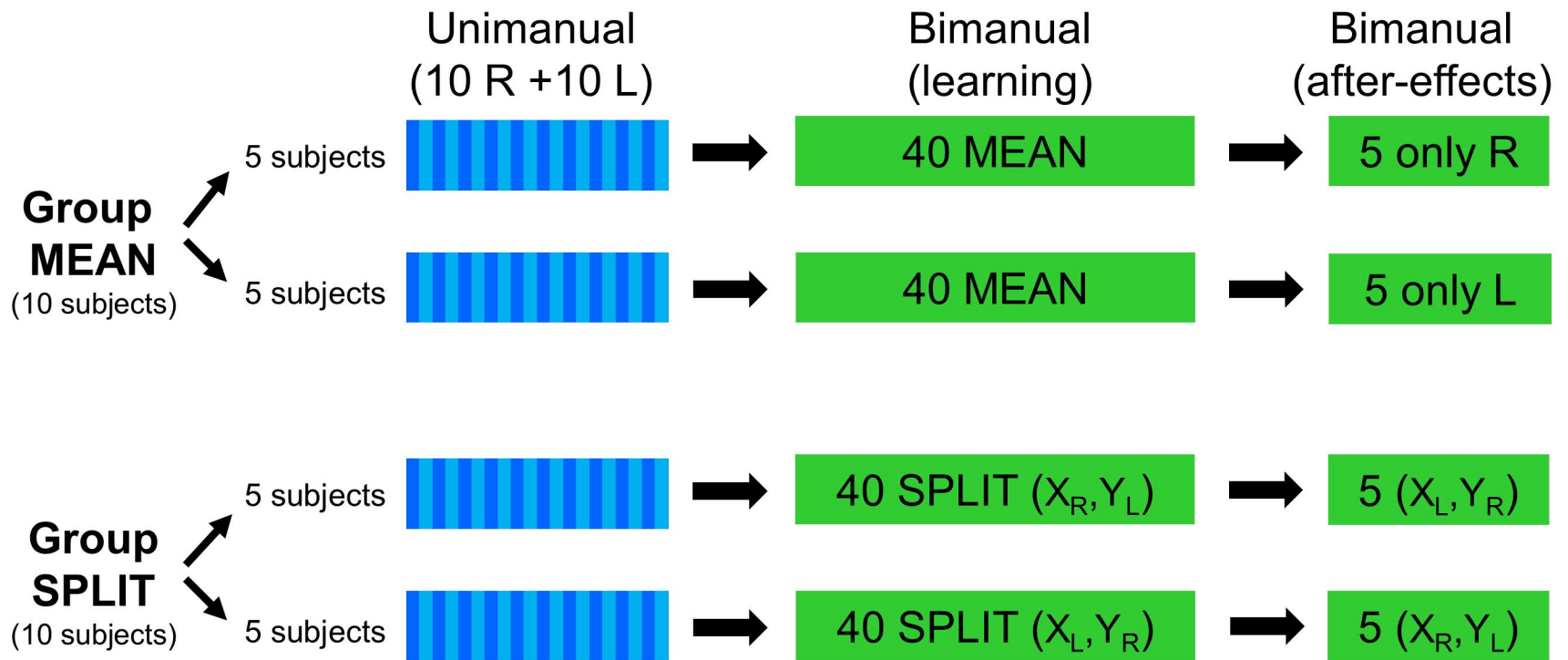
757

758 **Table 1.** Target trajectory parameters.

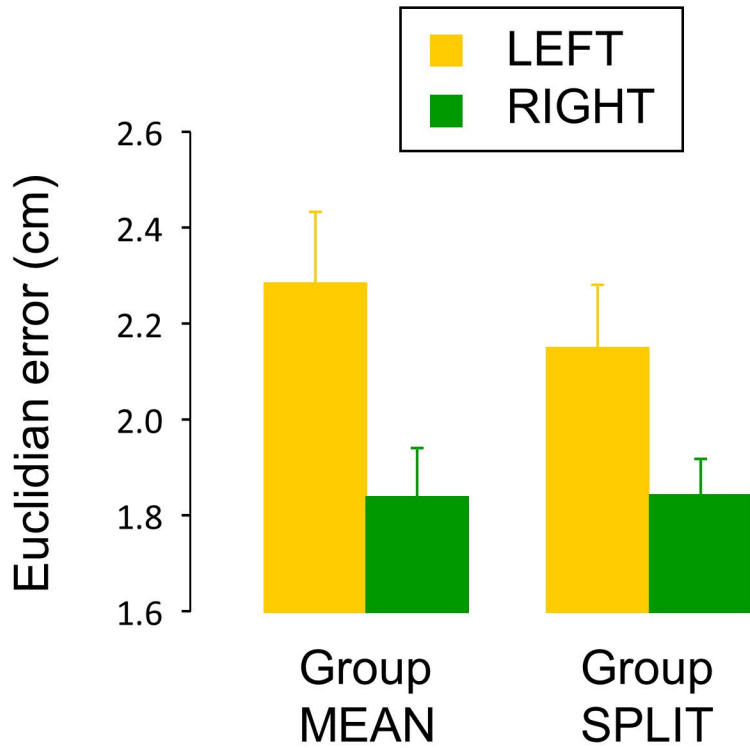
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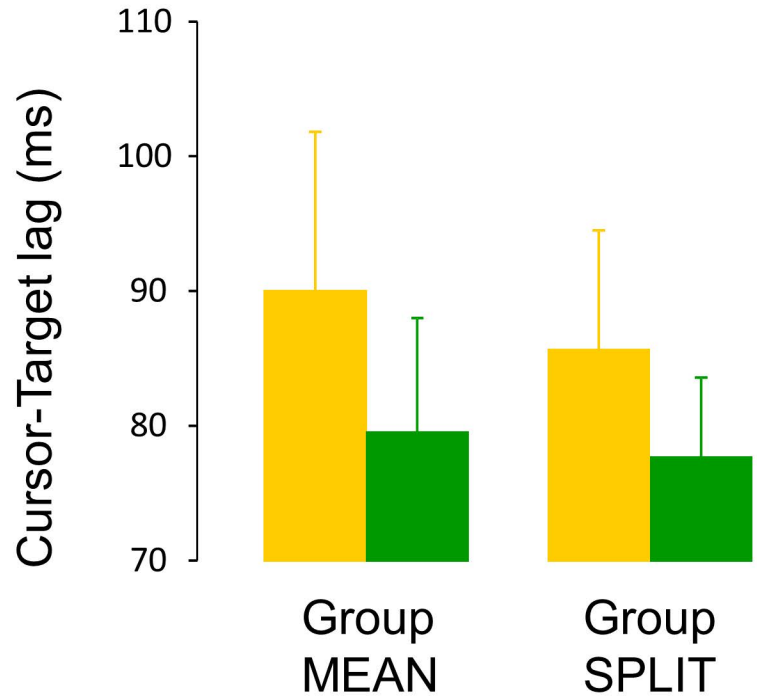




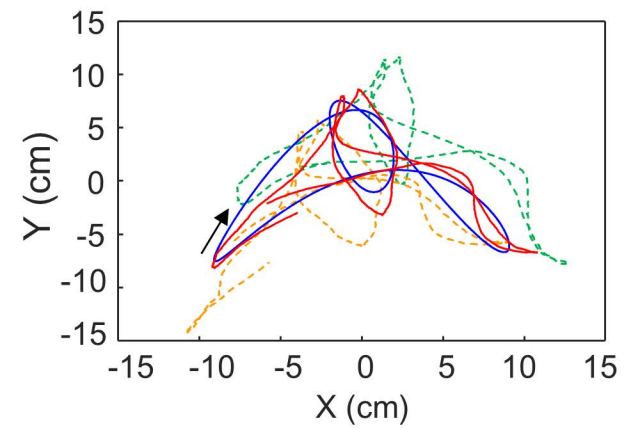
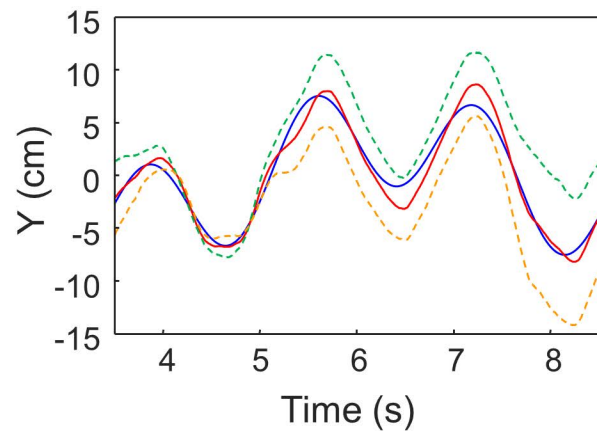
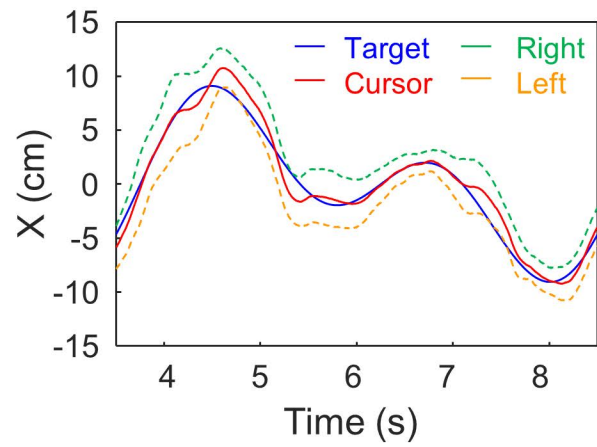
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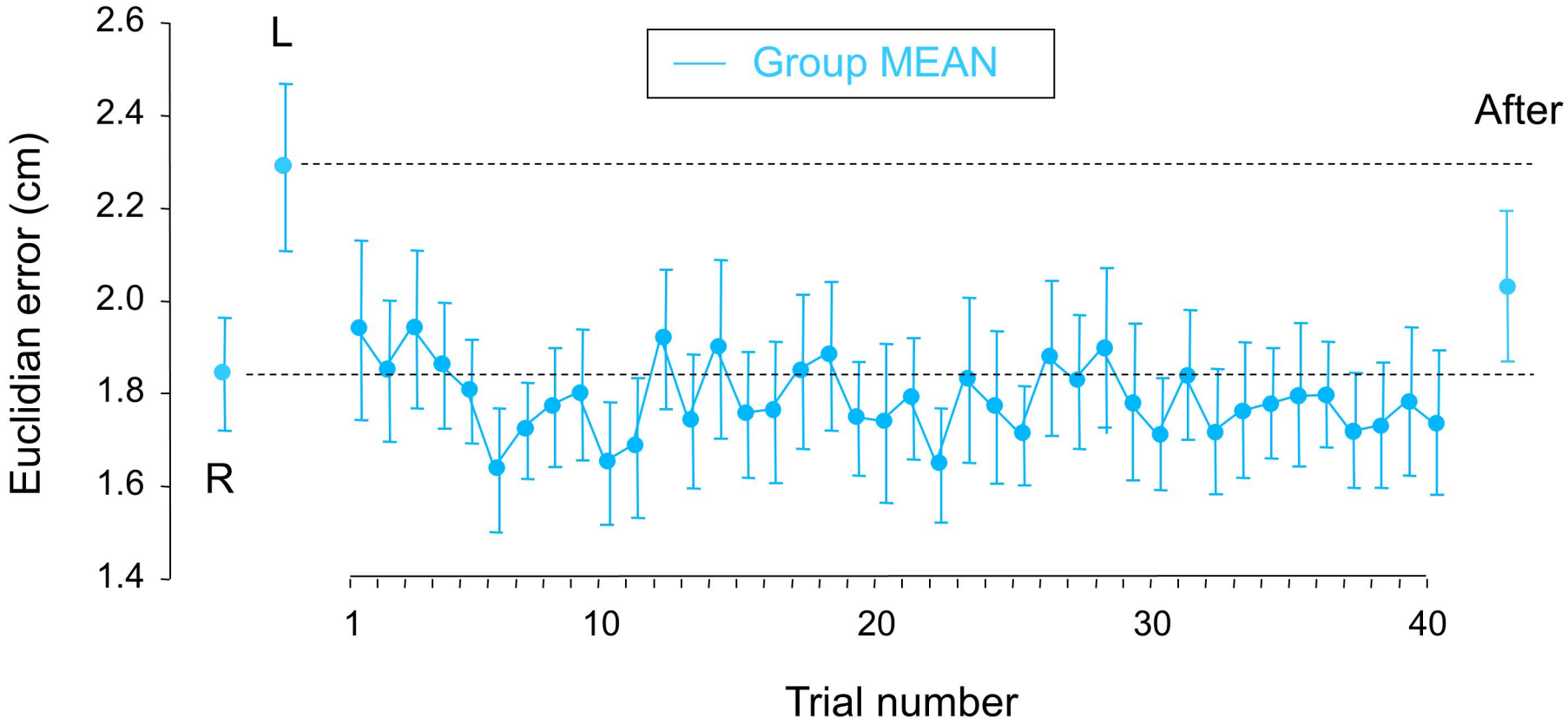


B

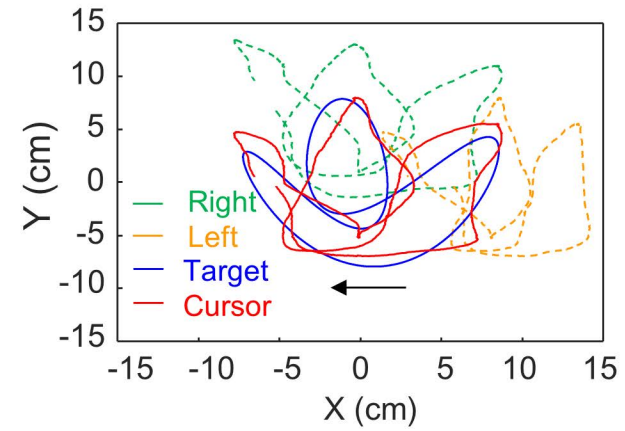
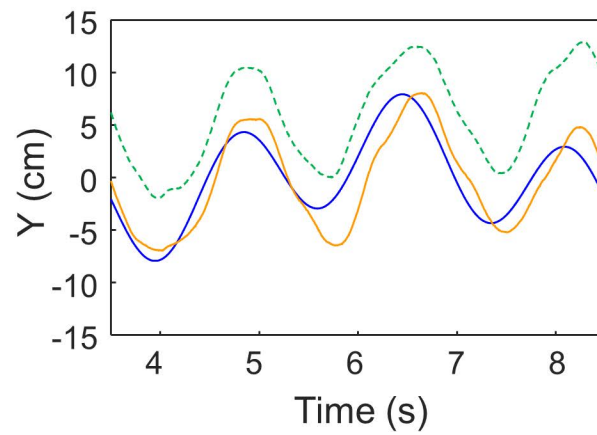
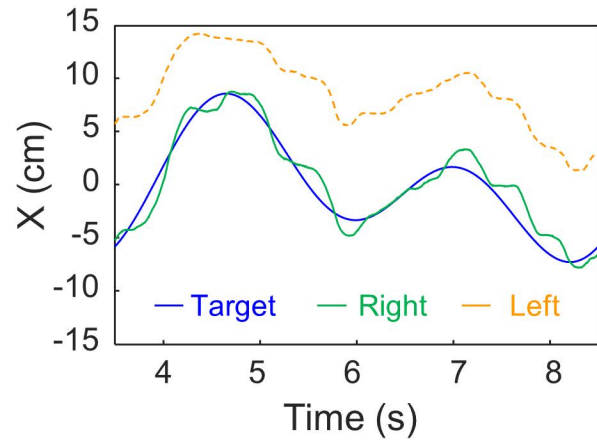


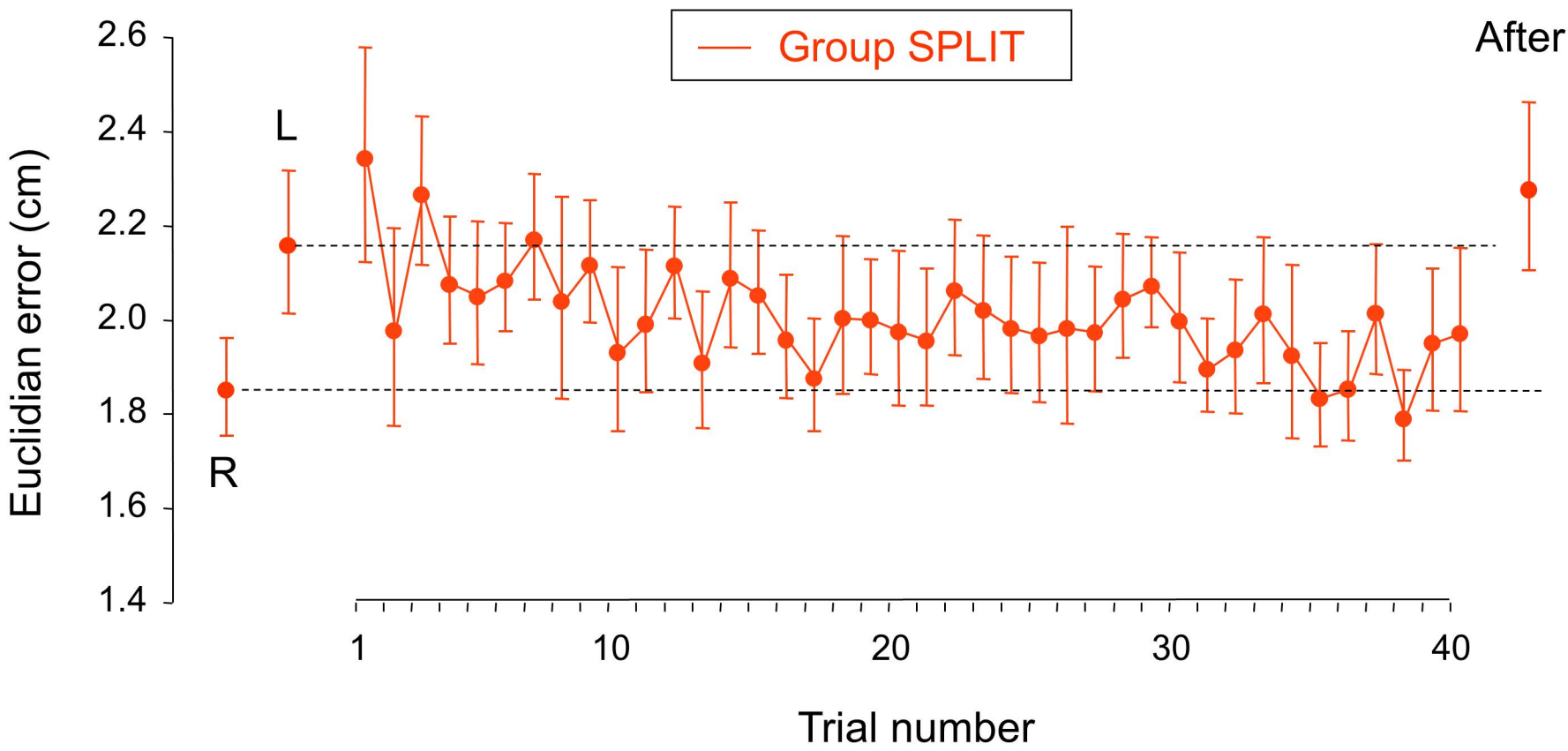
BIMANUAL MEAN



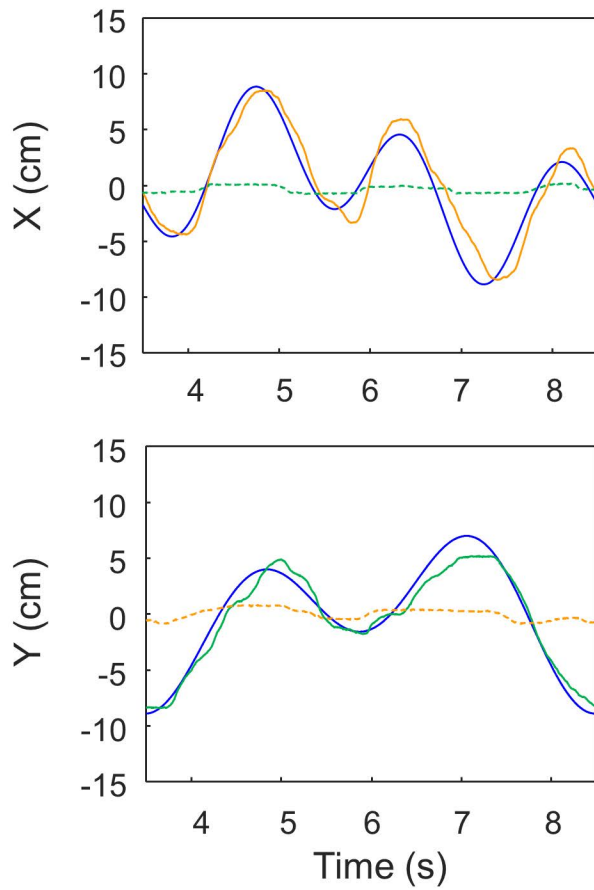


BIMANUAL SPLIT

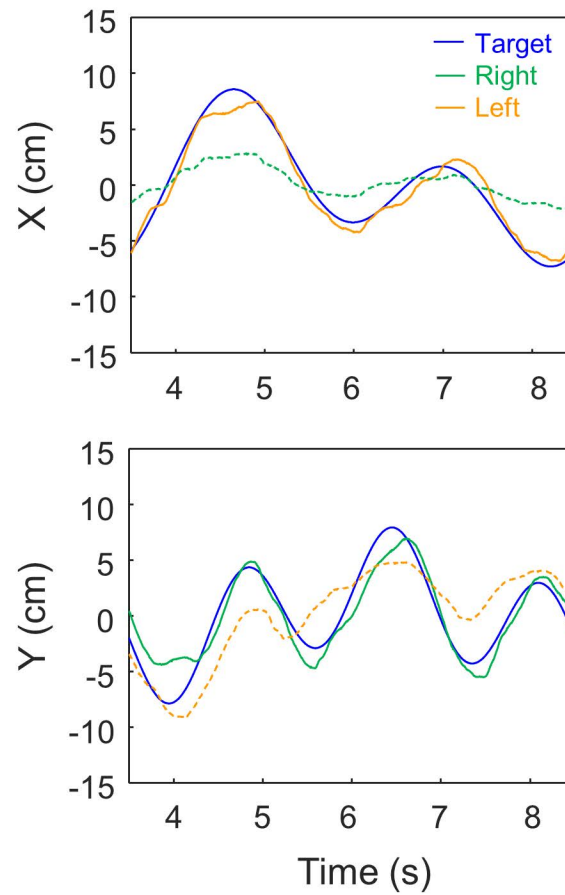


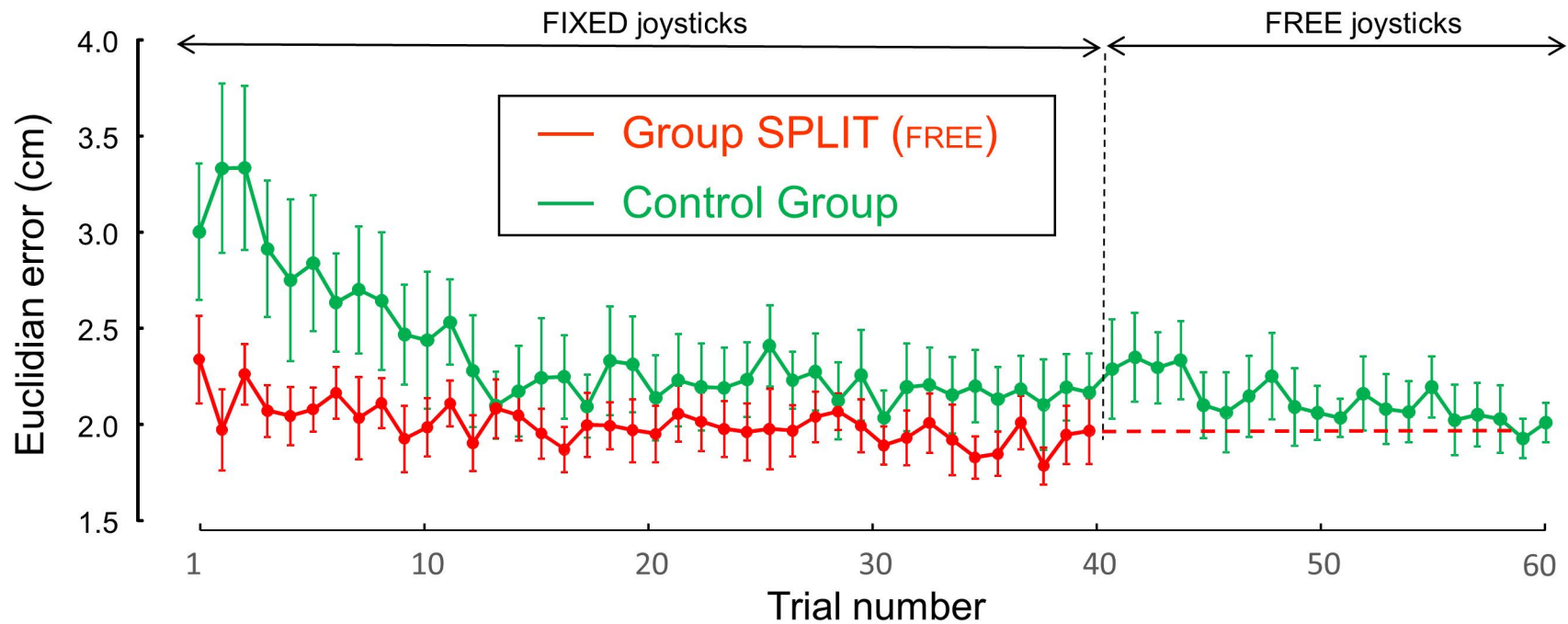
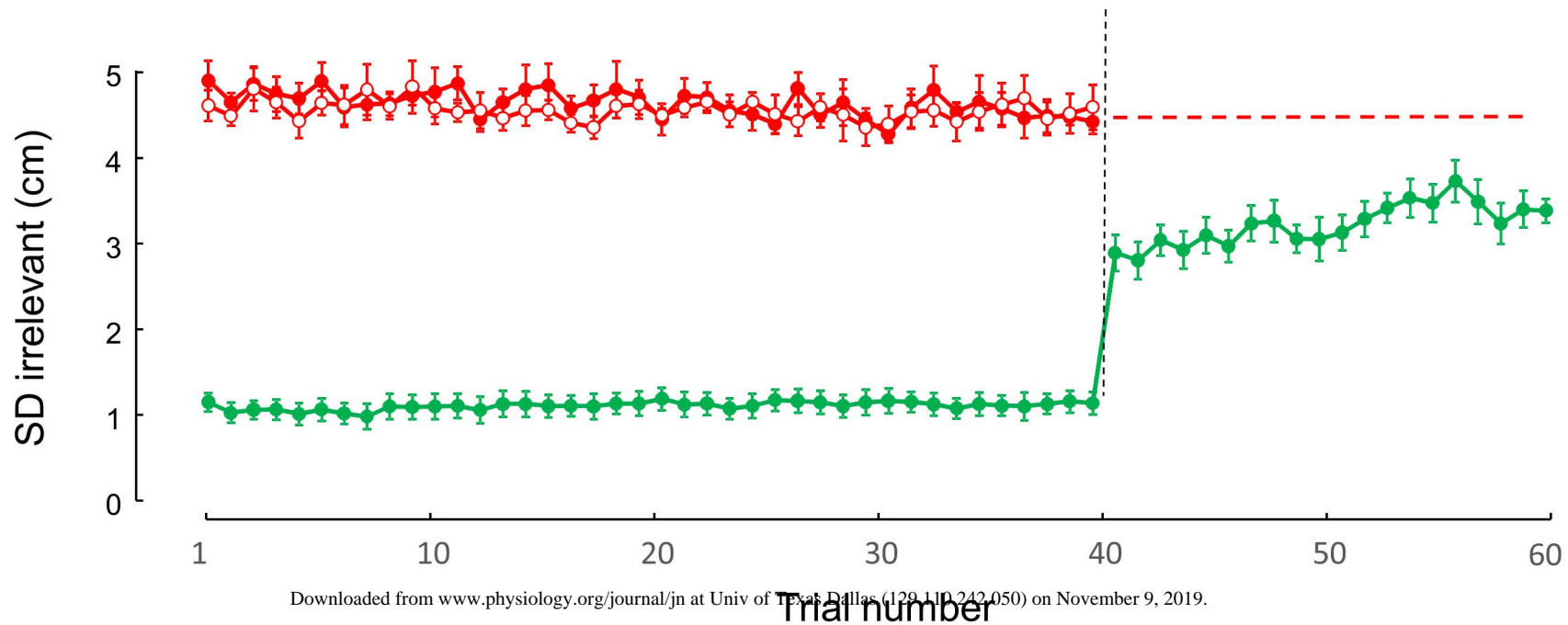


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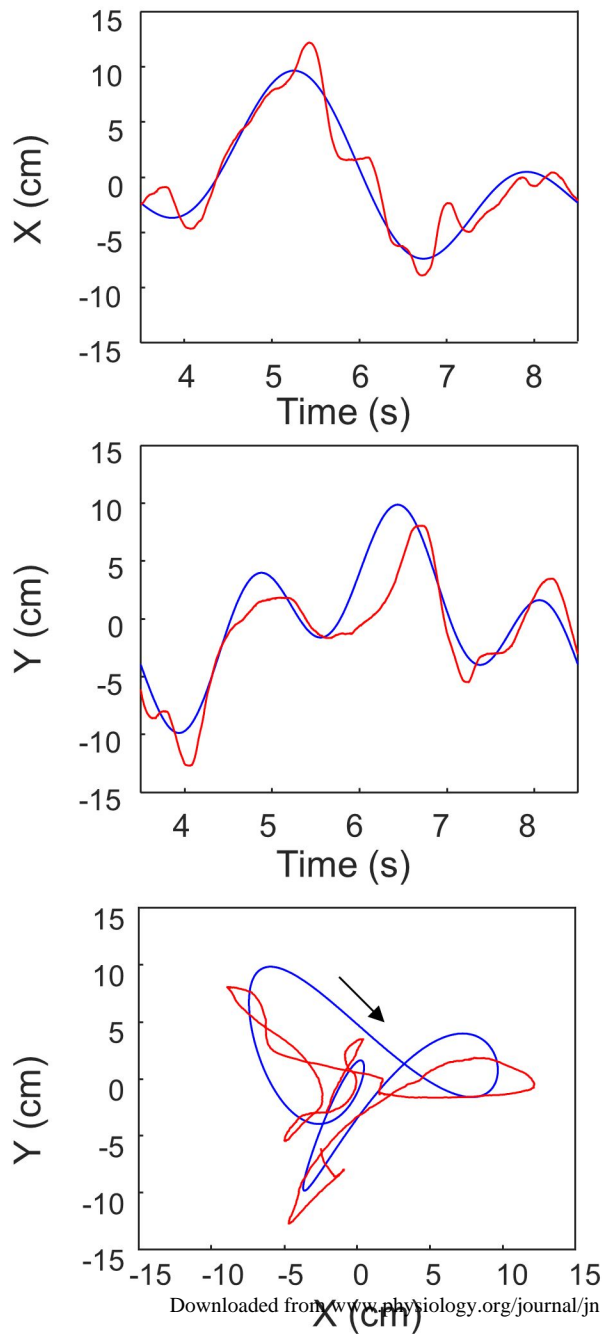


BIMANUAL SPLIT FREE

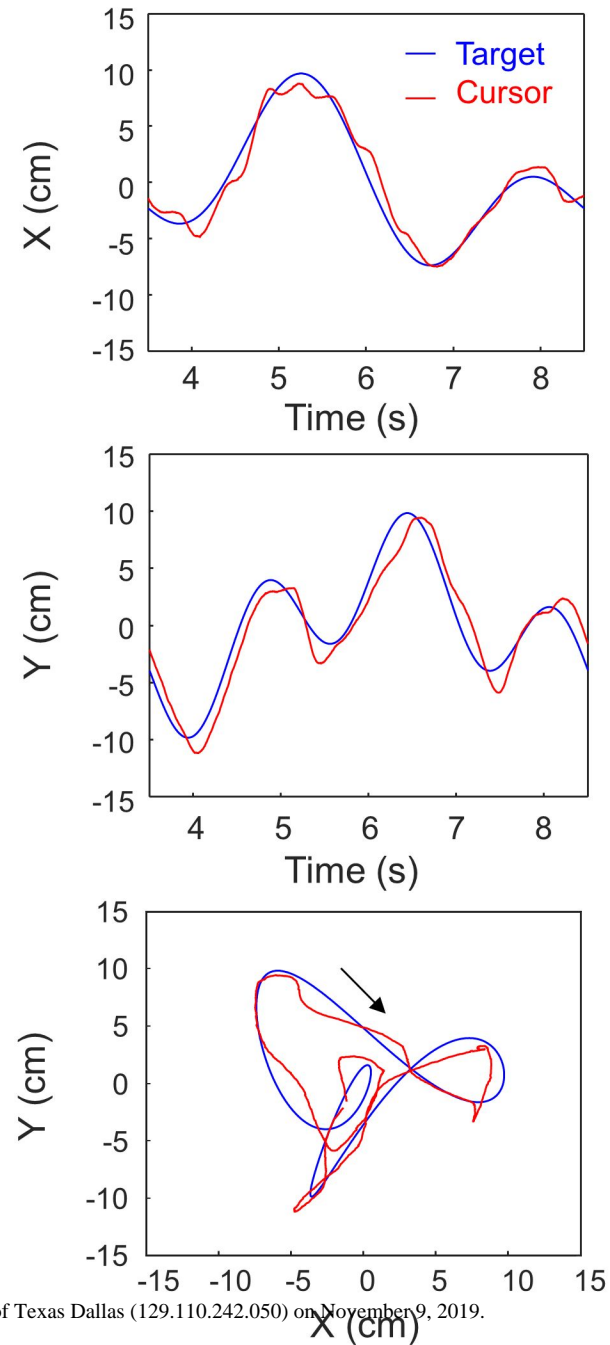


A**B**

UNIMANUAL-LEFT



UNIMANUAL-RIGHT



| 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 | 2 | -60 | 3 | 5 | 3 | -135 |
| 3 | 4 | 5.1 | 3 | -60 | 4 | 5.2 | 2 | -135 |
| 4 | 5 | 5 | 3 | 90 | 3.4 | 5 | 2 | 45 |
| 5 | 5.1 | 5.2 | 2 | -90 | 4 | 5 | 3 | 22.5 |