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RESEARCH ARTICLE | *Control of Movement*

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

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Mathew J, de Rugy A, Danion FR. How optimal is bimanual tracking? The key role of hand coordination in space. *J Neurophysiol* 123: 511–521, 2020. First published November 6, 2019; doi:10.1152/jn.00119.2019.—When coordinating two hands to achieve a common goal, the nervous system has to assign responsibility to each hand. Optimal control theory suggests that this problem is solved by minimizing costs such as the variability of movement and effort. However, the natural tendency to produce similar movements during bimanual tasks has been somewhat ignored by this approach. We consider a task in which participants were asked to track a moving target by means of a single cursor controlled simultaneously by the two hands. Two types of hand-cursor mappings were tested: one in which the cursor position resulted from the average location of two hands (Mean) and one in which horizontal and vertical positions of the cursor were driven separately by each hand (Split). As expected, unimanual tracking performance was better with the dominant hand than with the more variable nondominant hand. More interestingly, instead of exploiting this effect by increasing the use of the dominant hand, the contributions from both hands remained symmetrical during bimanual cooperative tasks. Indeed, for both mappings, and even after 6min of practice, the right and left hands remained strongly correlated, performing similar movements in extrinsic space. Persistence of this bimanual coupling demonstrates that participants prefer to maintain similar movements at the expense of unnecessary movements (in the Split task) and of increased noise from the nondominant hand (in the Mean task). Altogether, the findings suggest that bimanual tracking exploits hand coordination in space rather than minimizing motor costs associated with variability and effort.

NEW & NOTEWORTHY When two hands are coordinated to achieve a common goal, optimal control theory proposes that the brain assigns responsibility to each hand by minimizing movement variability and effort. Nevertheless, we show that participants perform bimanual tracking using similar contributions from the dominant and nondominant hands, despite unnecessary movements and a less accurate nondominant hand. Our findings suggest that bimanual tracking exploits hand coordination in space rather than minimizing motor costs associated with variability and effort.

bimanual; humans; manual tracking; optimal control; redundancy; visuomotor tracking

INTRODUCTION

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

Although a wide variety of tasks have been developed to explore the control of bimanual movements (Maes et al. 2017), the optimality of bimanual movement has been investigated using essentially two types of task. In the first task type, participants are asked to control a given force that corresponds to the (vectorial) sum of the force produced by each effector (Córdova Bulens et al. 2018; O'Sullivan et al. 2009; Salimpour and Shadmehr 2014). The results of these isometric studies are consistent with the view that force sharing is assigned with respect to minimization of noise and effort, depending on the context. Salimpour and Shadmehr (2014) reported a greater contribution of the less noisy dominant limb in a multijoint, two-dimensional force-aiming task, whereas O'Sullivan et al. (2009) found that effort minimization was more highly weighted than minimization of noise in a unidimensional force matching task. In the other type of task, participants are asked to make reaching movements by moving a cursor presented at the spatial average location of the two hands (Diedrichsen 2007; White and Diedrichsen 2010). Although this protocol elegantly showed that mechanical perturbation of one hand also triggers corrections in the nonperturbed hand (Diedrichsen 2007), it did not address the following two issues. First, we know that one hand is typically more accurate than the other for reaching (Mieschke et al. 2001; Roy and Elliott 1986;

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Schaffer and Sainburg 2017), and this asymmetry in performance has been shown to influence hand assignment (Córdova Bulens et al. 2018; Salimpour and Shadmehr 2014; White and Diedrichsen 2010). Second, Kelso et al. (1979) established that there is a strong natural coupling between hands when both are being moved simultaneously. In particular there is known preference both to activate homologous muscles across limbs (i.e., to move in the same direction in intrinsic muscle space) and to move limbs in the same direction in extrinsic task space (Diedrichsen et al. 2004; Howard et al. 2009; Swinnen et al. 1997, 1998). The goal of this study was to investigate how this bias for moving hands in the same direction in space might influence the putative minimization of effort and variability during a visuomotor tracking task performed with a two-handed cursor.

Our motivation for manual tracking lies in the fact that this task, in contrast to reaching a stationary target, requires constant adjustments of ongoing hand motor commands, thereby maximizing the contribution of online control. We reasoned that if optimal control can be considered a plausible, general theory of motor control, it should also account for bimanual visuomotor tracking. Visuomotor tracking was tested under two types of hand-cursor mapping. In the first mapping (Mean), we took inspiration from Diedrichsen (2007) so that the cursor position corresponded to the average spatial location of the two hands. In the second mapping (Split), we took inspiration from Neilson and Neilson (2002) and from Swinnen and colleagues (Puttemans et al. 2005; Vangheluwe et al. 2005) so that the vertical and horizontal positions of the cursor were controlled separately by the right and left hands. However, a key difference from earlier Split studies was that nonrelevant hand movements (i.e., movements that did not contribute to cursor motion) were permitted in our protocol, thereby allowing us to probe the subjects' behavior with respect to this redundant dimension. Finally, for control purposes, unimanual tracking under a conventional mapping was also investigated to characterize the tracking performance and variability associated with the dominant and nondominant hands.

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

MATERIALS AND METHODS

Participants. Twenty healthy right-handed volunteers (12 women; age: 26.8 ± 5.5 yr; hereinafter mean ± SD) were recruited. Handedness of participants was verified using the Oldfield Handedness Inventory (Oldfield 1971) with an average group laterality index of 95 ± 12. All participants gave written consent before participation. The experimental paradigm (2016-02-03-007) was approved by the local ethics committee of Aix Marseille University and complied with the Declaration of Helsinki. Each participant was compensated for his/her participation.

Data acquisition. Figure 1*A* shows the experimental setup. Participants were seated comfortably in a dark room facing a screen (BENQ; 1,920 × 1,080 pixels, 27-in., 144 Hz) positioned in the frontal plane 57 cm away from the participants' eyes. Participants' head movements were restrained by a chin rest and a padded forehead rest so that the eyes in primary position were directed toward the center of the screen. To block vision of their hands, a mask was positioned under the participants' chin. Depending on the conditions (see later), participants were required to hold one or two joysticks (Series 812; Megatron, Allinges, France; with ±25° of inclination along *x*-*y* axes) positioned horizontally on a table in front of them. Note that there was no restoring force to bring back the joystick at the central position. Moreover, the joysticks were frictionless and used conductive plastic technology, allowing quasi-infinite resolution. Both right and left forearms were resting on the table. The output of the joysticks was sent to a multichannel signal conditioner (MSC12; Entran, Fairfield, NJ) and was sampled at 1,000 Hz with a 16-bit resolution.

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

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

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

This technique was used to generate a pseudo-random two-dimensional pattern while preserving smooth changes in velocity and direction (Danion and Flanagan 2018; Mrotek and Soechting 2007; Soechting et al. 2010). A total of five different patterns were used throughout the experiment (see Table 1). The order of patterns was randomized across trials while making sure that each block of trials

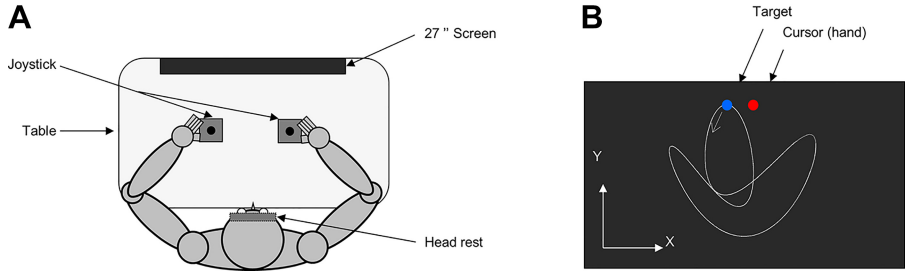

Fig. 1. Apparatus and experimental task. *A*: top view of a participant sitting in the experimental setup. *B*: schematic view of the screen during hand tracking. The target path was not displayed on the screen. (See MATERIALS AND METHODS for further information.)

Table 1. *Target trajectory parameters*

Trajectory	A_{1x}, cm	A_{2x}, cm	h_x	φ_x, °	A_{1y}, cm	A_{2y}, cm	h_y	φ_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

contained a similar number of each pattern. All trajectories had a period of 5 s (fundamental = 0.2 Hz).

A total of three hand-cursor mappings were tested. During unimanual trials, the relation between the joystick motion and its visual consequences on the screen was straightforward, mimicking the behavior of a computer mouse. During bimanual trials, the cursor position was driven by the motion of both joysticks. Two types of mapping could be employed. In the first mapping (Mean), the *XY* position of the cursor resulted from the average position of the right and left joysticks: $X = (X_R + X_L)/2$ and $Y = (Y_R + Y_L)/2$ (for a similar procedure see Diedrichsen 2007). In the second mapping (Split), each coordinate of the cursor was driven by a distinct joystick: either $X = X_R$ and $Y = Y_L$ or $X = X_L$ and $Y = Y_R$ (for a similar procedure see Neilson and Neilson 2002), although in this case movements of the joysticks along the nonrelevant axis were still possible). The gain of the joysticks was similar for all mappings with 25° inclination representing 15 cm (or 15° of visual angle) of cursor displacement on the screen. Each trial had a duration of 10 s (i.e., 2 cycles of the same trajectory). Overall, each participant performed 65 trials. Each experimental session took no more than 45 min.

Participants were divided into two groups that both successively performed uni- and bimanual trials. The experimental session consisted of three phases (see Fig. 2). During the initial phase, one group of participants (Mean group, $n = 10$) performed first one block of 20 unimanual trials, alternating trials by the right and left hand. Subsequently, this group performed one block of 45 bimanual trials. During the first 40 trials of this block, we employed the Mean mapping. During the last five trials, the unimanual mapping (i.e., only one joystick driving the cursor) was unexpectedly restored. Five participants from this group performed those last five trials with the contribution of the left joystick unexpectedly removed (as in right unimanual trials), and the other five with the contribution of the right joystick removed (as in left unimanual trials). The motivation for these catch-up trials was to assess whether the (eventual) coordination employed between hands in the bimanual task would be maintained even when it was no longer required.

The second group of participants (Split group, $n = 10$) followed a rather similar protocol with 20 unimanual trials (alternating right and left hands) followed by a block of 45 bimanual trials. The first 40 trials of this block were performed under the Split mapping, but during the last 5 trials the Split mapping was unexpectedly reversed (i.e., the contribution of each joystick was suddenly flipped) to assess the presence of aftereffects. Five participants in this group performed the first 40 bimanual trials with the left joystick controlling the *X*-axis and the right joystick controlling the *Y*-axis; during the last five trials, the left and right joystick controlled the *Y*- and *X*-axis, respectively. The opposite protocol was used for the other five subjects.

Just before participants performed bimanual trials, they were informed that the cursor motion would be driven by the combined action of the two joysticks. However, they were never informed about the underlying mapping linking the motion of the two joysticks and the motion of the cursor.

Control experiments. To provide further information about adaptation to the Split mapping, we tested another group of 10 right-handed participants (5 women; age: 26.1 ± 4.2 yr; laterality index: 91.9 ± 10.5) under the same mapping but with different settings of the joysticks. Specifically, these participants were asked to perform our bimanual Split tracking task using joysticks that were mechanically restrained to a single axis (one-dimensional instead of two-dimensional) by means of rails guiding the handle (for a similar procedure see Neilson and Neilson 2002). Additional measurements indicated that the stiffness of these rails was on the order of 3 N/cm, meaning that if a participant applied 3 N on the joystick's lever perpendicularly to the rails, the cursor could still move by 1 cm on the screen. Such scaling allows us to quantify the effort produced by the participants along the nonrelevant axes. As shown in Fig. 2, *bottom*, five participants experienced the Split mapping with X_R and Y_L, and the remaining five with the opposite mapping. Each participant completed a total of 60 trials under the same mapping, starting in a block of 40 trials with the guiding rails (fixed joysticks), followed by a block of 20 trials in which the rails were removed (free joysticks), allowing hand movements along the irrelevant axis for the task. The main motivation for this design was to investigate whether, after prolonged experience with the restrained joysticks, participants would be more effective at refraining from irrelevant movements when using the

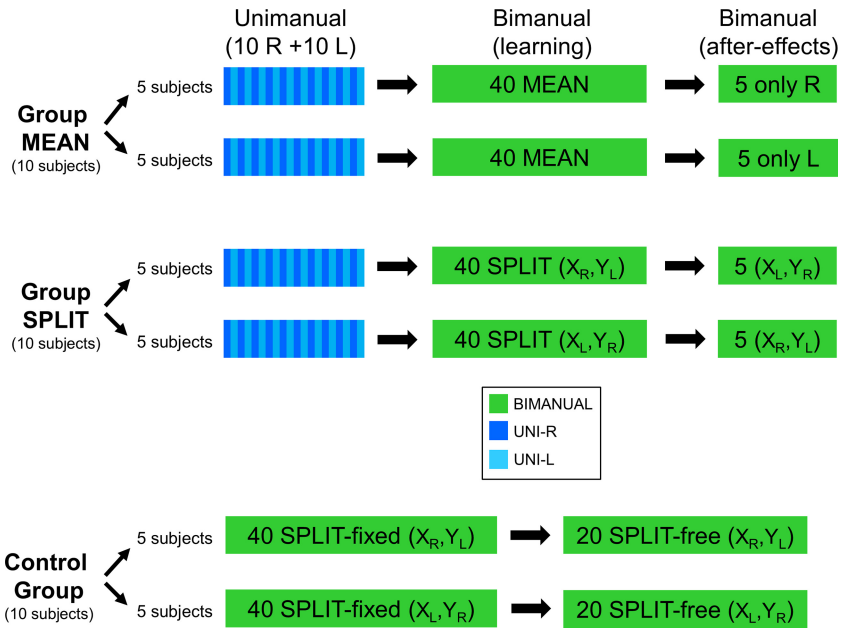

Fig. 2. Experimental design. L, left hand; R, right hand; Uni-L, left unimanual trial; Uni-R, right unimanual trial; X_L,Y_R, left joystick controlling the *X*-axis and right joystick controlling the *Y*-axis; X_R,Y_L, right joystick controlling the *X*-axis and left joystick controlling the *Y*-axis. (See MATERIALS AND METHODS for further information.)

unrestrained joysticks. Moreover, for this group, bimanual trials were not preceded by unimanual trials that could possibly prime homologous hand movements in extrinsic space.

As will be shown later, we observed that bimanual performance under Mean mapping led to better performance than left hand alone, and performance rather similar to right hand alone (if not better). Because in our previous protocol the bimanual condition was always performed after the two unimanual conditions, we decided to test another group of 12 right-handed participants (5 women; age: 26.6 ± 4.4 yr; laterality index: 90.0 ± 10.0) while ruling out any possible bias due to order effects. To achieve this goal, each participant completed one block of 20 trials successively with the left hand, the right hand, or both (Mean), but the order of the three blocks was counterbalanced across participants (6 possible orders, 2 subjects per order).

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

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

Statistics. Repeated-measure ANOVAs were used to assess the possible effects of hand (right/left), mapping (Split/Mean), and trials (first 3/last 3). The Newman–Keuls technique was used for post hoc tests to correct for multiple comparisons. A logarithmic (z score) transformation was used to normalize the distribution of R values. A 0.05 significance threshold was used for all analyses. Because the lack of significant differences across groups is not a validation of the null hypothesis, on a few occasions, we used Bayesian statistics with the JASP free software (https://jasp-stats.org) to quantify how true the null hypothesis was and report BF10 scores.

RESULTS

Unimanual tasks. Figure 3 plots two representative trials performed by the same participant when tracking the visual target with the right (dominant) or the left (nondominant) hand. As expected, manual tracking performance was more accurate with use of the right hand. Analyses of mean group cursor-target distance and cursor-target lag presented in Fig. 4 confirmed this trend. Indeed, two-way ANOVA (hand by group)

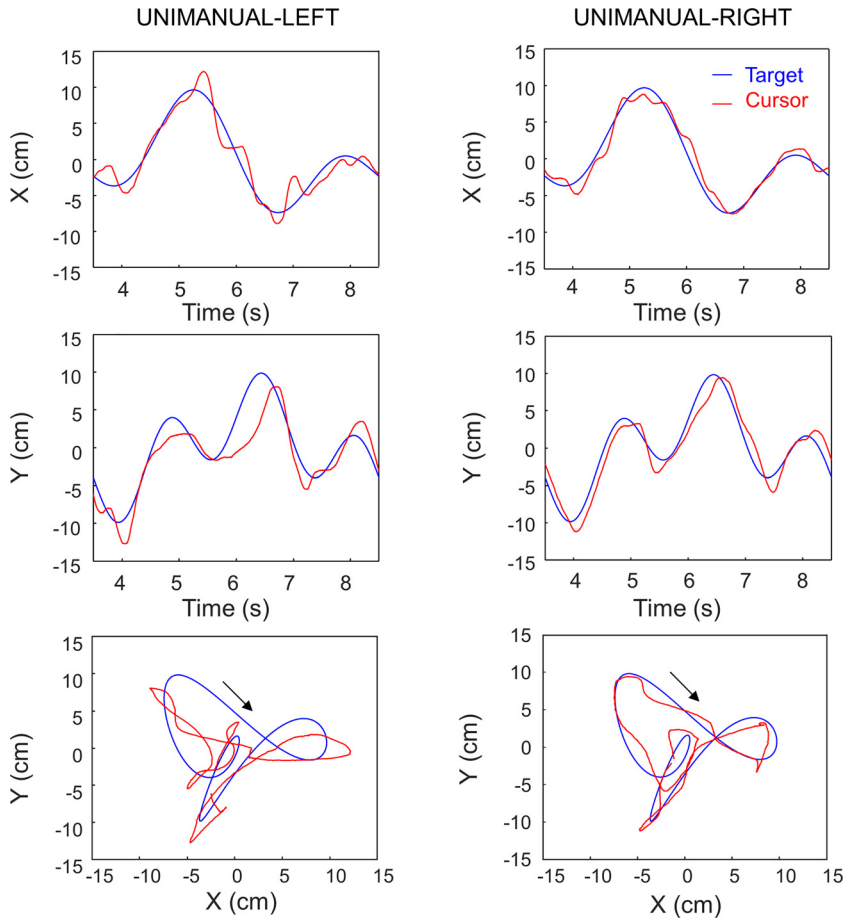

Fig. 3. Typical hand-tracking trials performed by the same participant under the same target trajectory. *Left* and *right* columns display cursor and target position when the joystick was moved with the left and right hand, respectively. *Top* and *middle* rows display respectively the horizontal (*X*) and vertical (*Y*) components of hand (cursor) and target motion. *Bottom* row displays the corresponding *XY* trajectories of cursor and target. Note the greater accuracy of hand tracking when the right (dominant) hand is used.

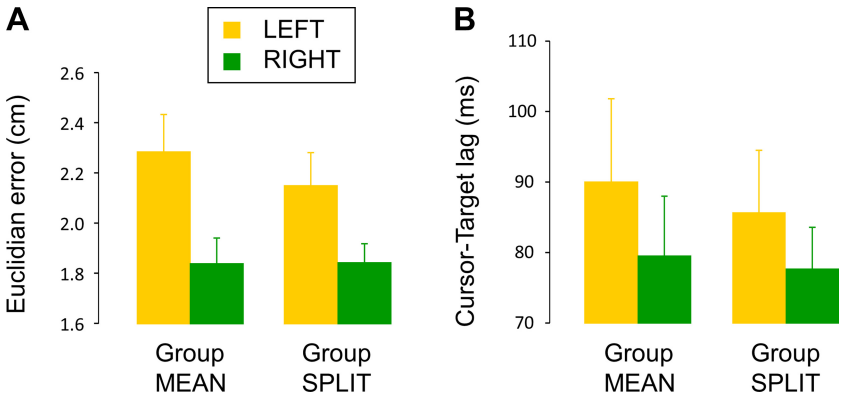

Fig. 4. Comparison between right and left hand performance during unimanual tracking. *A*: Euclidian distance between cursor and target in Mean and Split groups. *B*: temporal lag between cursor and target in Mean and Split groups. Error bars are SE. Note how tracking performance is consistently better for both groups when the right (dominant) hand is used compared with the left (nondominant) hand.

showed a main effect of hand [$F(1,18) = 53.12$, $P < 0.001$], with mean Euclidian distance between cursor and target being 20% greater when the left hand was used compared with the right hand (2.22 vs. 1.84 cm; see Fig. 4*A*). However, this ANOVA showed no significant differences across the two groups of participants [$F(1,18) = 0.17$, $P = 0.68$, $BF_{10} = 0.46$], nor was there a hand by group interaction [$F(1,18) = 1.81$, $P = 0.19$]. Regarding the temporal relationship between cursor and target (see Fig. 4*B*), we found that the lag was larger for the left hand than the right hand [90 vs. 80 ms; $F(1,18) = 6.59$, $P < 0.05$], but there was no significant effect of group [$F(1,18) = 0.07$, $P = 0.80$] and no interaction [$F(1,18) = 0.12$, $P = 0.73$]. Overall, these analyses confirm an effect of hand dominance (right-hand tracking is more accurate), as well as the homogeneity of our groups. The presence of homogeneity facilitates the interpretation of possible group differences as a consequence of manipulations of the hand-cursor mapping during the bimanual trials.

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

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

Figure 6 plots the average tracking performance as a function of trial rank. For comparison purposes, average unimanual performance is provided on the *left* side of the graph in Fig. 6. Averaged across the 40 trials, tracking performance under the Mean mapping (1.78 cm) was comparable to performance by the right hand alone [1.84 cm; $F(1,9) = 1.43$, $P = 0.26$, $BF_{10} = 0.61$], and thus smaller than that by the left hand alone [2.29 cm; $F(1,9) = 29.24$, $P < 0.001$]. Although tracking tended to improve across trials, with cursor-target distance decreasing from 1.91 to 1.75 cm between early trials (first 3) and late trials (last 3), the effect of trial did not reach significance [$F(1,9) = 2.60$, $P = 0.14$, $BF_{10} = 0.85$]. A similar pattern of results was observed when the cursor-target lag was examined. Indeed, there was no significant difference between the lag under the Mean mapping and the lag for the right hand alone [78 vs. 80 ms; $F(1,9) = 0.20$, $P = 0.66$, $BF_{10} = 0.41$]. However, the lag under the Mean mapping was marginally smaller than for the left hand alone [78 vs. 90 ms; $F(1,9) = 4.33$, $P = 0.06$].

With regard to bimanual coordination, analyses showed that motion of the two joysticks was strongly correlated both in time and in extrinsic space. Indeed, averaged across trials, the correlation coefficient between the joysticks was 0.84 and 0.90, respectively, for the *X* and *Y* components ($P < 0.001$). Analysis of the temporal lag between the two joysticks revealed that neither the right nor the left hand was leading the other, because this lag was not significantly different from 0 [$t(9) = 0.63$, $P = 0.54$; mean 4.8 ± 7.6 ms]. When the total

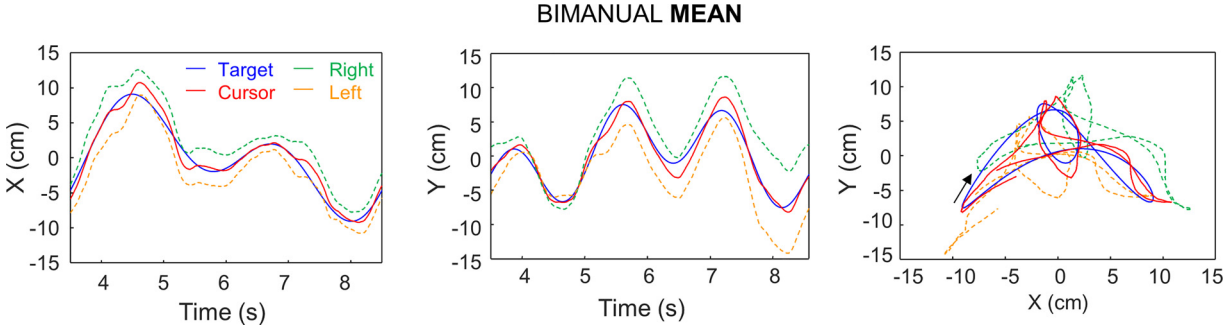

Fig. 5. Typical bimanual trial under the Mean hand-cursor mapping. *Left* and *middle* graphs display respectively the horizontal (*X*) and vertical (*Y*) components of each hand, cursor, and target movement. *Right* graph displays the corresponding *XY* trajectories of cursor and target. Signals that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

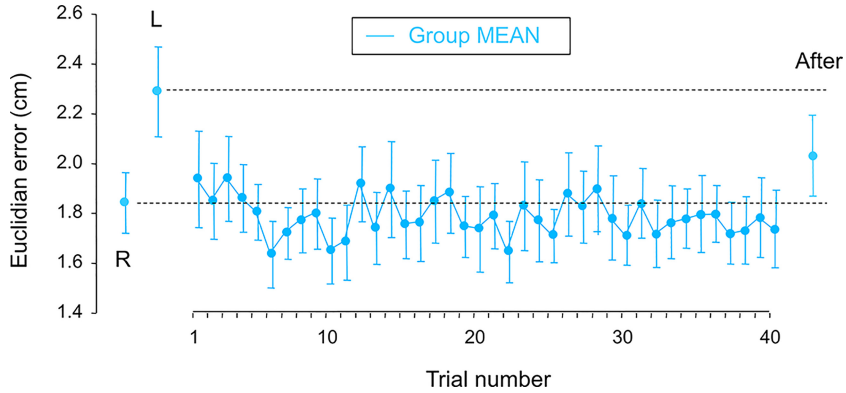

Fig. 6. Mean tracking performance under the Mean bimanual condition as a function of trial number. Error bars are SE. For comparison purposes, average unimanual performance is shown at *left*. L, left hand; R, right hand.

distances covered by each joystick were compared, no significant difference was found between the right and the left hands, for movements along either the *X*-axis [104.6 vs. 108.9 cm; $F(1,9) = 0.56$, $P = 0.47$, $BF_{10} = 0.52$] or the *Y*-axis [112.1 vs. 110 cm; $F(1,9) = 0.11$, $P = 0.74$, $BF_{10} = 0.43$]. Taken together, these observations are not consistent with a greater involvement of the right hand than the left, as would be predicted if participants were attempting to minimize motor noise.

When the Mean mapping was unexpectedly removed so that only one hand was now in control of the cursor, we observed an overall increase in tracking error. This increase follows from the fact that half of the participants controlled the cursor with the right hand, whereas the other half used the left hand. Indeed, average tracking performance during catch trials (2.03 cm) was not different from the average tracking performance when all unimanual trials involving either right or left hands alone were pooled (2.06 cm). Moreover, despite the fact that only one hand became useful to move the cursor, participants persisted in making similar movements in extrinsic space with both hands. Indeed, the correlation between joysticks was 0.82 and 0.85, respectively, for the *X* and *Y* components during the catch trials ($P < 0.001$).

Because we were intrigued that bimanual performance under Mean mapping could lead to performance rather similar to that for the right hand alone (if not better), we run a control experiment in which the order of the conditions was counterbalanced. Although this new data set confirmed that the right hand was more accurate than the left hand [1.59 vs. 1.96 cm; $F(1,11) = 36.91$, $P < 0.001$], it appears that the benefit provided by the bimanual condition was smaller than initially observed. Indeed, in this experiment, bimanual performance (1.67 cm) was somewhat intermediate, meaning that it was better than for the left hand alone [$F(1,11) = 35.28$, $P < 0.001$] but worse than for the right hand alone [$F(1,11) = 9.83$, $P < 0.01$]. Overall, it appears that bimanual tracking may have benefited from earlier practice under the unimanual conditions in our former experiment.

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

As can be seen on the typical Split trial displayed in Fig. 7, despite the fact that the right hand had no influence over the *X* cursor position and the left hand had no influence over the *Y* cursor position, both right and left hands performed irrelevant movements along these axes while remaining strongly coupled. Figure 8 plots the average tracking performance, with unimanual performance on the *left* side for comparison purposes. Average Split performance (2.00 cm) was marginally worse than unimanual performance with the right hand [1.85 cm; $F(1,9) = 3.92$, $P = 0.07$] but better than unimanual performance with the left hand [2.15 cm; $F(1,9) = 7.77$, $P < 0.05$]. Altogether Split performance was equivalent to average performance of pooled unimanual control tasks involving only right-hand or left-hand movements (2.00 cm). We also noticed a marginal effect of trial [$F(1,39) = 1.4$, $P = 0.06$], suggesting improvements in tracking performance between early and late trials. A similar pattern of results was observed when the cursor-target lag was examined. Indeed, we found that the temporal lag under Split mapping (82 ms) was comparable to

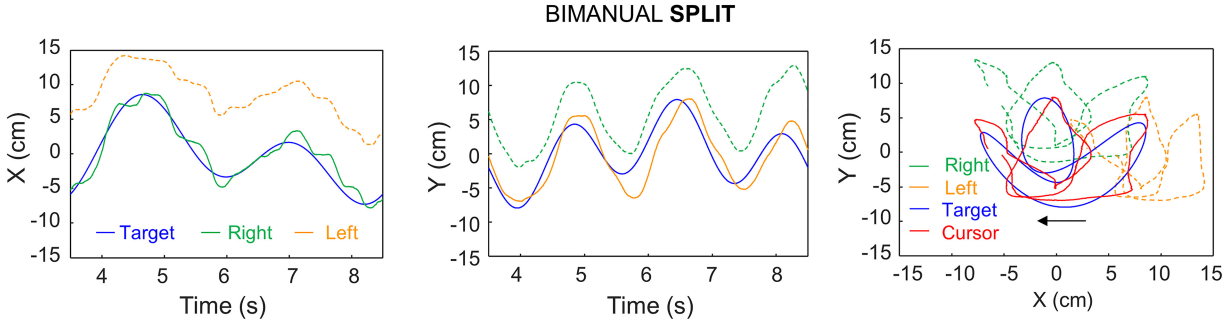

Fig. 7. Typical bimanual trial under the Split hand-cursor mapping. *Left* and *middle* graphs display respectively the horizontal (*X*) and vertical (*Y*) components of each hand, cursor, and target movement. *Right* graph displays the corresponding *XY* trajectories of cursor and target. Signals that were not displayed on the screen are represented by dashed lines. Note how similar are the right and left hand motions.

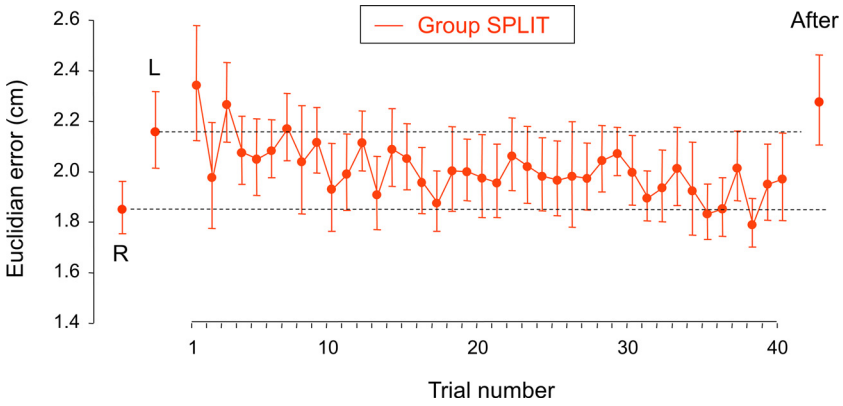

Fig. 8. Mean tracking performance under the Split bimanual condition as a function of trial number. Error bars are SE. For comparison purposes, average unimanual performance is shown at *left*.

the average lag observed when the right and left hand were used in isolation (78 and 86 ms, respectively).

Despite the fact that tracking under Split conditions could encourage dissociated hand movements, the motion of the right and left joysticks remained strongly correlated throughout the 40 trials, demonstrating that participants failed to assign a separate contribution to each hand. Indeed, averaged across trials, the average coefficient correlations between joysticks were 0.85 and 0.89, respectively, for the *X* and *Y* components ($P < 0.001$). Regarding the temporal lag between the two joysticks, neither the right nor the left hand led the other; this lag was not significantly different from 0 [$t(9) = 1.23$, $P = 0.25$; mean 8.5 ± 6.9 ms]. Analyses of the total distance covered along the relevant and irrelevant axes showed no significant difference. Indeed, the total distance covered along the *X*-axis was similar whether joystick movement was relevant or not [108.7 vs. 104.7 cm; $F(1,9) = 0.97$, $P = 0.35$, $BF_{10} = 0.61$]. A similar observation was made when relevant and irrelevant distances covered along the *Y*-axis were compared [112.6 vs. 110.6 cm; $F(1,9) = 0.133$, $P = 0.72$, $BF_{10} = 0.41$]. Overall, participants failed to suppress irrelevant hand movements under Split mapping and performed the task while maintaining similar hand movements in extrinsic space, an observation that does not support a scheme of effort minimization in this task.

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

To assess whether the production of irrelevant movements would be reduced after prior training with restrained (unidirectional) joysticks, we tested another group of participants (Control group; Fig. 9). Figure 10*A* shows the time course of tracking accuracy when these participants used restrained and then unrestrained joysticks. For comparison purposes, the tracking accuracy of participants who only practiced with the unrestrained joysticks (Split group) was added. As can be seen, the initial tracking performance of the Control group was

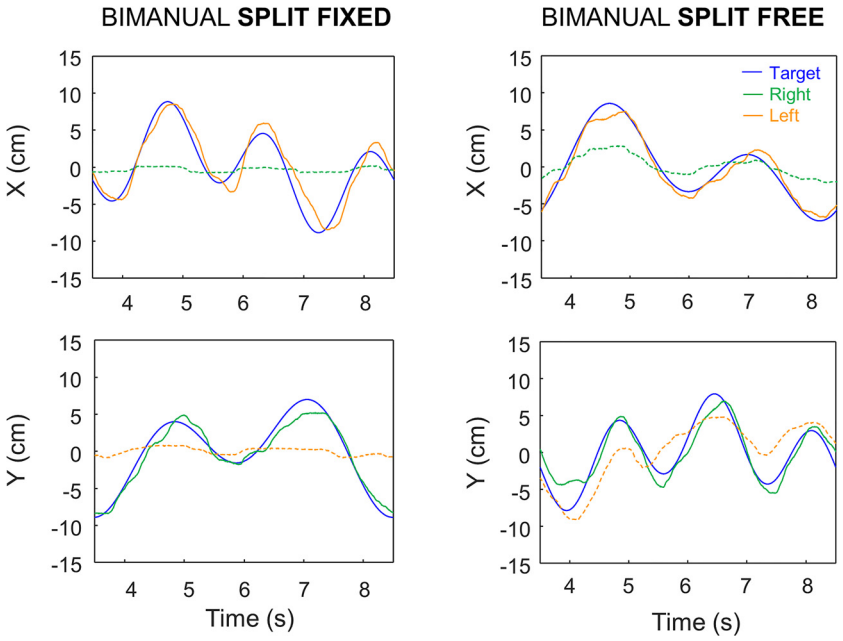

Fig. 9. Typical Split bimanual trials during the control experiment. *Left* column displays 1 trial performed when participant used the restrained joysticks (i.e., that could only move along one axis; Split fixed). *Right* column displays 1 follow-up trial when the same participant employed the unrestrained joysticks (i.e., free to move in 2 dimensions; Split free). *Top* and *bottom* rows display respectively the horizontal (*X*) and vertical (*Y*) components of each hand, cursor, and target movement. Signals that were not displayed on the screen are represented by dashed lines. Note the presence of irrelevant hand motion when the unrestrained joysticks were used.

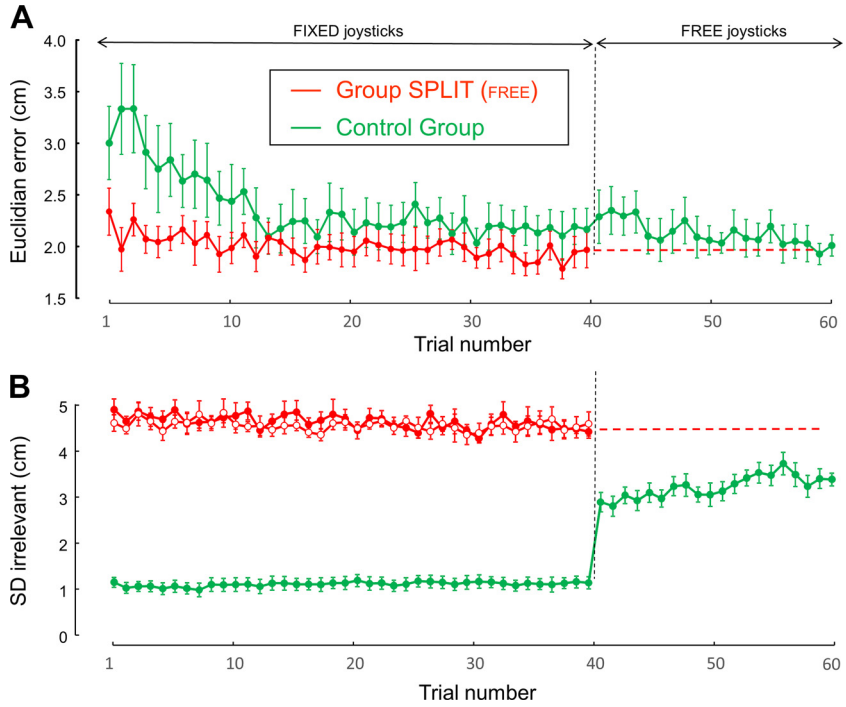

Fig. 10. Comparison between tracking performance with and without the rails on the joysticks. *A*: Euclidian error as a function of trial number in group using unrestrained joysticks [red; Split (free)] and in the Control group (green). *B*: same as *A* for the SD of hand movements along the irrelevant axis. For comparison purposes, SD of hand movements along the relevant axis are presented as open red circles for Split group. The red dashed lines provide an extension of Split group computed over the last trial. Note how irrelevant hand movements built up immediately after the removal of the rails in the control group. Error bars are SE.

worse than the performance of Split group, thereby suggesting that the task became more difficult under dissociated movements. During the first three trials, the Euclidian distance between cursor and target was, respectively, 3.22 and 2.19 cm for the Control group and Split group, an almost 50% difference [$F(1,18) = 6.21$, $P < 0.05$]. However, following 40 trials of practice, participants of the Control group improved their tracking skill such that their performance (last 3 trials) became closer to that of Split group participants [2.16 vs. 1.90 cm; $F(1,18) = 1.19$, $P = 0.29$, $BF_{10} = 0.60$]. Moreover, further improvement was observed when participants switched from restrained to free joysticks. Indeed, when the first three and last three trials with the free joysticks were compared, the Euclidian distance decreased from 2.27 to 2.01 [$F(1,9) = 6.92$, $P < 0.05$]. Thanks to those extra 20 trials with the free joysticks, tracking performance of the Control group became even more similar to that of the Split group [2.01 vs. 1.90; $F(1,18) = 0.38$, $P = 0.54$, $BF_{10} = 0.46$].

An important issue is whether extended practice with the restrained joysticks favors the suppression of irrelevant hand movements during subsequent use of the free joysticks. In Fig. 10*B*, we present the time course of irrelevant hand movements as measured by the SD of the joysticks along the irrelevant axis. As can be seen, during the session with the restrained joysticks, the SD remained close to 1 cm. Thanks to our estimation of the rail's stiffness, this SD suggests contact forces of ~3 N, a value substantially higher than the force typically employed to maneuver the unrestrained joysticks (~0.1 N). As soon as the joysticks were freed, irrelevant hand movements strongly increased and kept growing with further practice. When the first three and the last three trials with the free joysticks were compared, SD increased from 2.91 to 3.34 cm [$F(1,9) = 6.92$, $P < 0.05$]; for comparison purposes, the SD for relevant and irrelevant movements of the Split group were 4.55 and 4.63 cm, respectively. Finally, a significant negative correlation between Euclidian error and irrelevant SD was found across the 20 trials with the free joysticks ($R = -0.58$, $P < 0.01$), suggesting that irrelevant hand movements facilitated hand tracking. Altogether, these results show that despite prolonged practice promoting dissociated hand movements, participants were still unable to suppress irrelevant hand movements when subsequently using unrestrained joysticks. Moreover, the production of irrelevant movements was associated with better tracking performance. Overall, the analyses of irrelevant hand movements, with both the restrained and unrestrained joysticks, do not support a minimization of effort in our bimanual task.

DISCUSSION

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

Failure to assign separate hand contributions under Mean. In agreement with earlier studies, we found that unimanual tracking was more accurate with the dominant hand (Aoki et al. 2016; Carey et al. 2003; Simon et al. 1952). Moreover, the asymmetry in manual dexterity observed in our study (+20% error in the left hand compared with the right hand) fits rather well with previous studies investigating the optimality of bimanual behavior using isometric tasks that require one either to reach a given force level with the fingers pressing on transducers (+23–35% in O'Sullivan et al. 2009) or to generate a force vector with the arms using handles (+18% in Salimpour and Shadmehr 2014). Assuming that optimal performance is reflected by the minimal sum of squared errors, we predicted that the contribution of the right hand should be 44% greater than the contribution of the left hand, an asymmetry that would be consistent with earlier studies (O'Sullivan et al. 2009; Salimpour and Shadmehr 2014). However, our observations failed to support this scheme, and participants performed the task with both hands contributing equally to target motion. Moreover, kinematic analyses revealed that hand motions were tightly coupled in time and space, with both hands making similar and synchronous movements in extrinsic space. Overall, our results do not support the view of a greater contribution by the less noisy hand. What can be the reason(s) leading to different effects of handedness in our task and in earlier studies? We see two options that relate to the motoric aspects of the task. First, in the studies of O'Sullivan et al. (2009) and Salimpour and Shadmehr (2014), participants had to produce isometric forces with the fingers or the arms, whereas our study required actual movements of the hands to maneuver the joysticks. However, it remains unclear why minimizing variability would be more critical for isometric than for isotonic tasks. Perhaps the mapping between force and cursor feels more arbitrary (and hand specific) than the mapping between position and cursor. Another difference relates to the continuous/discrete nature of the tasks involved. In the studies of O'Sullivan et al. (2009) and Salimpour and Shadmehr (2014), participants had to produce discrete reaching movements ($<$1 s), which contrasts with the longer continuous tracking movements required in our study (10 s). It is possible that different involvements of feedforward and/or planning mechanisms, as well as constant online adjustments associated with tracking an unpredictable stimulus, might have limited the expression of optimization processes.

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

Taken together, our observations obtained with the Split mapping and free joysticks, as well as during and after practice with the restrained joysticks, suggest that minimizing effort was not a key factor in determining the pattern of bimanual coordination selected by participants. What could be the reason(s) leading to these counterintuitive observations? One possibility is that the energetic cost of wrist movements associated with manipulating our frictionless joysticks might be marginal, especially when compared with the energetic cost associated with full-arm reaching movements (Córdova Bulens et al. 2018; Diedrichsen 2007; Salimpour and Shadmehr 2014). As a result, one could argue that minimization of effort did not operate in our task because there was virtually no effort involved. Although this argument may hold for the persistence of irrelevant movements with free joysticks (force $\approx$0.1 N), it is less obvious why, when using the restrained joysticks, participants applied much stronger forces for irrelevant movements ($\approx$3 N) than relevant ones, especially considering that the minimization of effort has been found to operate for comparable finger forces (O'Sullivan et al. 2009). Alternatively, it is possible that, in the absence of hand movements, forces applied against the rails provided somatosensory feedback facilitating bimanual coordination. Future experiments using joysticks with haptic feedback may be helpful in clarifying whether increasing the load associated with the motion of the joysticks promotes the minimization of effort. Finally, as previously proposed for the minimization of variability, it is possible that the minimization of effort was more challenging when constant adjustments of hand movements were required in our bimanual tracking task.

On optimality and the natural tendency to coordinate both hands in space. So far our results provide little evidence that effort and variability, two quantities repeatedly reported to be optimized during unimanual as well as bimanual reaching (Emken et al. 2007; Franklin et al. 2008; Gaveau et al. 2014; Mistry et al. 2013; O'Sullivan et al. 2009; Salimpour and Shadmehr 2014), are optimized during bimanual tracking. These results are consistent with some reaching studies showing that subjects maintain suboptimal behavior under altered mechanical contexts, even after prior experience of the optimal solution (Ganesh et al. 2010; Kistemaker et al. 2010). Indeed, despite having learned to perform the task with dissociated hand movements in our control condition, unnecessary movements (i.e., along the irrelevant dimension) emerged as soon as the mechanical constraints preventing those movements were released. Instead of optimizing behavior for every set of novel task constraints, the nervous system might therefore take advantage of its existing behavioral repertoire (Loeb 2012; de Rugy et al. 2012). In this context, it is important to note that although performance with restrained joysticks approached performance with unrestrained joysticks, they still did not quite equate. This observation is consistent with an additional cost inherent to the production of dissociated hand movements and

fits well with a brain imaging study showing increased activity for dissociated than for coupled right-left finger movements (Meister et al. 2010). Moreover, the correlation found between performance improvement and the amount of irrelevant hand movements on release of the mechanical constraint reflects a benefit associated with the natural tendency to coordinate hands in space. In the context of rhythmic bimanual movements, natural coordination patterns are known to depend on a coalition of both intrinsic and extrinsic constraints, whereby coordination that involves synchronous muscle contractions and/or synchronous movements in space is more stable (Salesse et al. 2005). In the context of reaching adaptation, there is also evidence for simultaneous representation of sensorimotor transformation for both hands in intrinsic as well as extrinsic coordinate systems. Indeed, interlimb transfer following sensorimotor adaptation in one limb was immediate and maximized when intrinsic and extrinsic reference frames were aligned for the two limbs (Carroll et al. 2014, 2016). The natural tendency to couple the two hands in space is therefore likely to have constrained our bimanual tracking tasks such that the benefits of exploiting this natural tendency outweighed the motor costs associated with unnecessary movements along irrelevant dimensions and the preferential use of the more accurate dominant hand.

Limitations. In the present study we tested the adequacy of optimal control theory for bimanual tracking on the basis of minimizing the sum of squared errors, using an equation provided by O'Sullivan et al. (2009) in the context of a task in which participants had to press against a one-dimensional load cell. As a result, one may wonder to what extent this equation applies to our two-dimensional tracking task in which motor noise may exhibit different dynamics depending on hand movement direction. Although models can be adjusted to account for directional anisotropies of motor noise during reaching to static targets (see *Eq. 8* in Salimpour and Shadmehr 2014), this is less obvious in our task in which the target was constantly changing direction and speed. Moreover, even if we had conducted a separate experiment to properly assess how tracking performance might vary along each individual direction and speed, it would still remain unclear how this behavior applies to the context where both parameters are constantly changing. Although possible directional asymmetries in hand tracking need to be explored, further data processing in our study already reveals that the right hand advantage is similar along the horizontal and vertical axes, suggesting that the right-left hand asymmetry is rather direction insensitive. Overall, the contribution of the current study is clearly not on the modeling aspect, but in making the general point that bimanual tracking involves additional constraints of hand coordination in space rather than the mere minimization of variability and effort.

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

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DISCLAIMERS

This paper reflects only the authors' view and that the Research Executive Agency (REA) of the European Commission is not responsible for any use that may be made of the information it contains.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

J.M., A.d.R., and F.R.D. conceived and designed research; J.M. performed experiments; J.M. and F.R.D. analyzed data; J.M., A.d.R., and F.R.D. interpreted results of experiments; J.M. and F.R.D. prepared figures; J.M., A.d.R., and F.R.D. drafted manuscript; J.M., A.d.R., and F.R.D. edited and revised manuscript; J.M., A.d.R., and F.R.D. approved final version of manuscript.

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