

# Prior movement of one arm facilitates motor adaptation in the other

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## 16 **Abstract**

17 Many movements in daily life are embedded in motion sequences that involve more than one limb,  
18 demanding the motor system to monitor and control different body parts in quick succession. During  
19 such movements, systematic changes in the environment or the body might require motor adaptation  
20 of specific segments. However, previous motor adaptation research has focused primarily on motion  
21 sequences produced by a single limb, or on simultaneous movements of several limbs. For example,  
22 adaptation to opposing force fields is possible in unimanual reaching tasks when the direction of a prior  
23 or subsequent movement is predictive of force field direction. It is unclear, however, whether multi-limb  
24 sequences can support motor adaptation processes in a similar way. In the present study, we investi-  
25 gated whether reaches can be adapted to different force fields in a bimanual motor sequence when the  
26 information about the perturbation is associated with the prior movement direction of the other arm. In  
27 addition, we examined whether prior perceptual (visual or proprioceptive) feedback of the opposite arm  
28 contributes to force field-specific motor adaptation. Our key finding is that only active participation  
29 in the bimanual sequential task supports pronounced adaptation. This result suggests that active seg-  
30 ments in bimanual motion sequences are linked across limbs. If there is a consistent association between  
31 movement kinematics of the linked and goal movement, the learning process of the goal movement can  
32 be facilitated. More generally, if motion sequences are repeated often, prior segments can evoke specific  
33 adjustments of subsequent movements.

## 34 35 **Significance statement**

36 Movements in a limb's motion sequence can be adjusted based on linked movements. A prerequisite is  
37 that kinematics of the linked movements correctly predict which adjustments are needed. We show that  
38 use of kinematic information to improve performance is even possible when a prior linked movement  
39 is performed with a different limb. For example, a skilled juggler might have learned how to correctly  
40 adjust his catching movement of the left hand when the right hand performed a throwing action in a  
41 specific way. Linkage is possibly a key mechanism of the human motor system for learning complex  
42 bimanual skills. Our study emphasizes that learning of specific movements should not be studied in  
43 isolation but within their motor sequence context.

## 44 **1 Introduction**

45 Many movements in daily life are embedded in motion sequences that involve more than one limb. In-  
46 teraction between two arms in frequently repeated sequences is usually fast and effortless. For example,  
47 a juggler is able to transfer juggling balls rapidly and precisely between two hands. Due to variability in  
48 single motor segments, the juggler has to be able to adjust movements accordingly. In the current study,  
49 we investigate how the motor system is able to learn such intricate mechanisms to adjust movements in

50 bimanual sequences. We show that once a motor sequence is learned, kinematic information from the  
51 beginning of the sequence can be used to modify later segments.

52 If two or more movements in a sequence are repeated in the same order many times, the individual  
53 motor elements seem to be linked together in a single motor action ([Diedrichsen and Kornysheva, 2015](#);  
54 [Verwey et al., 2015](#)). Thus, a motor element which is strongly linked in a sequence can influence prior  
55 and following motor segments ([Hansen et al., 2018](#)). If a reach is linked to a prior movement of the same  
56 arm, kinematic characteristics of that prior movement can even facilitate motor adaptation ([Howard  
57 et al., 2012](#)). In other words, information from a preceding same-limb movement can be used to adjust  
58 the following movement accordingly.

59 Motor adaptation studies involving a single force field have shown that an internal model of the  
60 motor dynamics to counteract external forces is acquired over time ([Anwar et al., 2011](#)). When multiple  
61 force fields are experienced, interference problems arise. Simple visual cues that indicate perturbation  
62 direction are ineffective in eliciting motor adaptation to opposing force fields (e.g., [Cothros et al.,  
63 2009](#)). In contrast, cues that allow overcoming the interference of multiple force fields are related to  
64 the motor plan ([Hirashima and Nozaki, 2012](#); [Howard et al., 2017](#); [Sarwary et al., 2015](#); [Sheahan et al.,  
65 2016](#); [Waincott et al., 2005](#)) or the sensory state of the arm ([Howard et al., 2013](#); [Green and Labelle,  
66 2015](#); [Sarwary et al., 2013](#); [Crevecoeur et al., 2022](#)). Such cues are thought to enable cue-specific  
67 motor memory formation and retrieval by putting the sensorimotor system in the right preparatory  
68 state ([Howard et al., 2020](#)). Linked movements in particular seem to be effective cues because the  
69 representation of the entire motor sequence is specific to each perturbation direction and thus allows  
70 the creation of separate sensorimotor memories for each force field. In addition, sensory same-arm  
71 movement cues – passive or visual prior movements – are as effective for field-specific adaptation as  
72 actively performed linked movements ([Howard et al., 2012](#)). This suggests that perceptual information  
73 that implies the sensory consequences of same-arm movement execution can be linked to the active  
74 target reach.

75 Bimanual motor adaptation research, however, has been focused primarily on simultaneously exe-  
76 cuted movements rather than sequential movements ([Tcheang et al., 2007](#); [Howard et al., 2008](#); [Kadota  
77 et al., 2014](#); [Nozaki et al., 2006](#)). Therefore, despite its relevance for human motor behavior, it is yet  
78 unknown if a prior opposite-arm movement can serve as an effective cue for force field specific adap-  
79 tation. Successful adaptation would indicate that distinct sequential segments of bimanual sequences  
80 can be linked together. During juggling this would mean that, for instance, specific kinematics of the  
81 throwing action of one arm could be linked to specific adjustments during the catching motion of the  
82 other arm.

83 In the present study we, thus, investigated linkage of movements of two arms. In addition to the  
84 replication of previous unimanual findings, we examined whether, and to what extent, a prior movement  
85 of the opposite arm could facilitate adaptation of the following movement in a force field interference

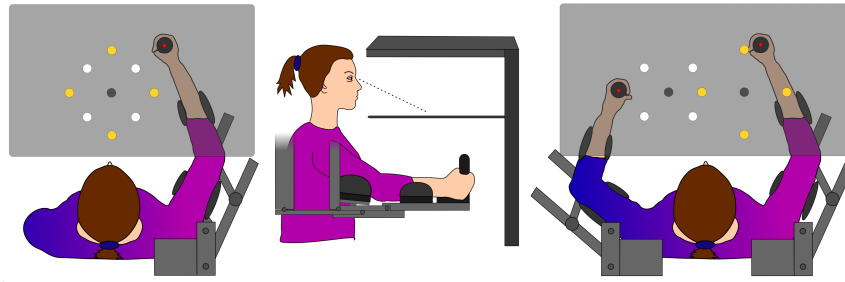


Figure 1: **Experimental setup.** Kinarm Exoskeleton Robot Lab. All possible target positions are shown. The screen is displayed transparent here; however, in the experiment participants were not able to see their arms. Left: Setup unimanual groups. Middle: Side view. Right: Setup bimanual groups.

86 task. To answer what aspects are key for establishing a link between such movements, we tested whether  
87 prior sensory information from the other arm (vision or proprioception) could be used as an effective  
88 cue for force field specific adaptation.

## 89 2 Materials and Methods

90 Our study design, including sample sizes, hypotheses and main analysis plan, was pre-registered on OSF  
91 (<https://osf.io/qy9rn>). Data and analysis scripts we used to arrive at the results we present here will be  
92 made available upon publication. In total, 68 right-handed volunteers aged 18-35 years (34 female, 34  
93 male) participated in our study. We excluded 4 participants from analysis (see below), thus our sample  
94 comprised 64 (32 female, 32 male,  $M_{age} = 26$ ,  $SD_{age} = 4.3$ ) participants. All participants had normal or  
95 corrected-to-normal vision and were free of any known neurological, perceptual and motor impairments  
96 and disorders. The experiment was approved by the local ethics committee of the University of Leipzig.  
97 Participants gave informed written consent prior to the experiment.

98 All participants were required to make reaching movements in a Kinarm Exoskeleton Lab (see  
99 Figure 1; for a video of the task see OSF repository). The Kinarm Exoskeleton Lab is a robotic device  
100 that can measure movements of the arms in the horizontal plane at a sampling rate of 1000 Hz. The  
101 robot can apply forces to the arms and provide visual feedback in a two-dimensional augmented virtual  
102 environment.

### 103 2.1 Experimental Design

104 Participants were randomly assigned to one of five groups (see Figure 2). Each group performed reaches  
105 to targets in the Kinarm. In two of the five groups, participants were required to move only their right  
106 arm (unimanual groups), while the other three groups incorporated both hands in subsequent reaching  
107 movements (bimanual groups). In the unimanual groups, three targets were displayed during each  
108 trial: the cue, middle and final target (see Figure 3A). The middle target was individually calibrated  
109 to be at the position of the hand when the elbow was flexed 90° and the shoulder angle was 60°. In  
110 the bimanual groups, there were four targets: the cue, middle-left, middle-right and final target. The

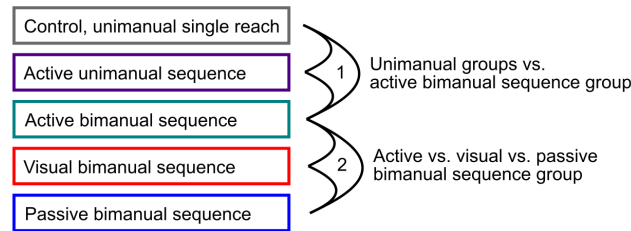


Figure 2: **Experimental groups and comparisons.** All groups and planned comparisons between groups to answer 1) whether and to what extent the effectiveness of a prior arm movement to allow force field specific adaptation generalizes to bimanual sequences and 2) whether prior sensory information from the other arm in one modality (vision or proprioception) can be used instead of active movement for force field specific adaptation.

111 distance between the two middle targets was 18 cm, and the midway point between them was fixed at  
112 90° elbow and 60° shoulder angle for each participant. Each trial consisted of one or two active reaches.  
113 The final reach in each trial was the same for all experimental groups: participants made a reaching  
114 movement from the middle or middle-right target to the final target with their right hand.

115 In all groups, there were four possible final target positions: 12 cm to the right, left, up or down  
116 from the middle (-right) target. There were two possible cue positions for each final target position  
117 (see Figure 3B). The distance between cue and middle (-left) target was 10 cm. The cursor displaying  
118 current hand position was red and 0.5 cm in diameter. All targets were 1.25 cm in diameter. The final  
119 target was yellow. All other targets were initially grey and changed their color to white during the trial  
120 (see below).

121 All groups went through three experimental phases: baseline, adaptation, and washout (see Fig-  
122 ure 3C). Bimanual groups went through two additional experimental phases thereafter, namely re-  
123 adaptation and another washout phase. These latter two phases aimed at assessing potential transfer  
124 of learning from different bimanual sequence group conditions to a bimanual group condition which  
125 involved actively moving both arms.

126 During trials in the adaptation and re-adaptation phases, a velocity-dependent curl field was present  
127 between the middle (-right) and the final targets. This force field systematically perturbed the right  
128 hand's movements. The force field started with a ramp up time of 100 ms once the right hand was more  
129 than 2 cm away from the midpoint of the middle target and stopped once the final target had been  
130 reached. The cue's location in relation to the final target was uniquely associated with the direction  
131 of the force field. Half of the participants learned the association between a positive angle between  
132 cue and final target and a clockwise (CW) force field, the other half between a positive angle and  
133 a counterclockwise (CCW) force field to control for any kinematic or biomechanical advantages of a  
134 specific combination. The association between the sign of the angle and the direction of the force field  
135 was fixed for each participant and did not change during the experiment.

136 The forces experienced during adaptation trials were perpendicular to movement direction and

137 proportional to reaching velocity:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = c \begin{bmatrix} 0 & -1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix}$$

138 where the constant  $c$  was set to  $-13$  Ns/m or  $+13$  Ns/m depending on the location of the cue (Howard  
139 2012). The resulting force field was CW or CCW, respectively. There was never a force field between  
140 the cue and the middle target(s) and there was never any force field present in baseline or washout  
141 trials.

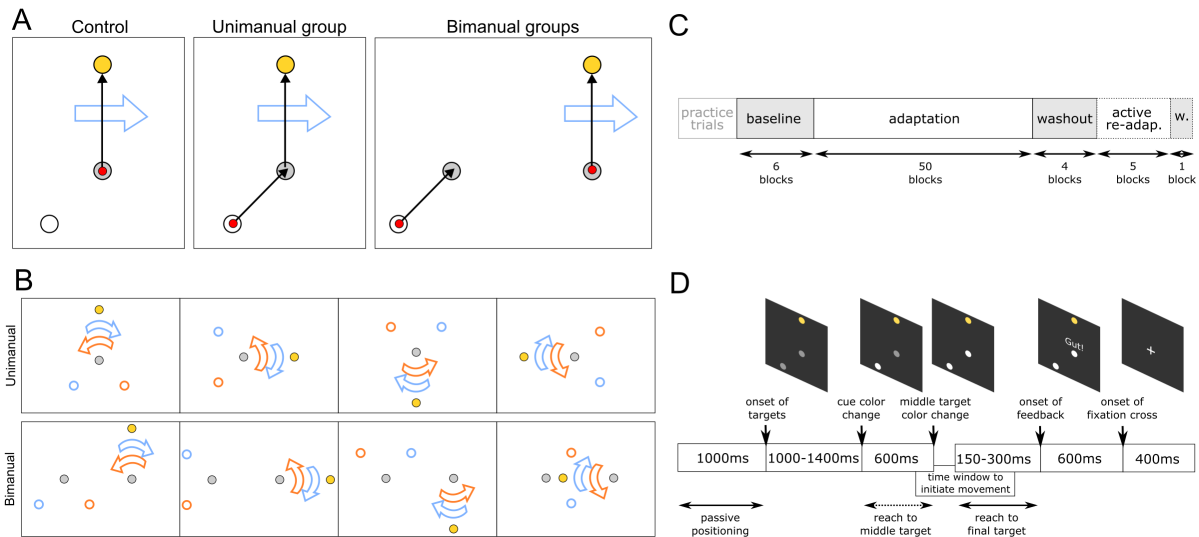
142 In 11% of trials, chosen randomly throughout the trial sequence, the Kinarm forced movements to  
143 be straight by means of a force channel, that is, a force field that resembles a straight channel with  
144 impenetrable walls on its sides. In these trials, no curl force field was present. We term these trials  
145 clamp trials, as they restrict participants movements to a straight trajectory while they attempt to  
146 counteract the expected (but absent) force field perturbation. The Kinarm measures the compensatory  
147 forces applied by the participant against the channel walls during the clamp trial, allowing us to quantify  
148 any possible feed-forward learning, which would be expressed in the compensation of the expected (but  
149 absent) force field. Due to technical constraints, clamp trials did not always generate a strong enough  
150 force channel. In this case, the hand broke through the virtual wall and deviated from the straight  
151 trajectory. We excluded these trials, and so analysis of the last four adaptation block was based on 422  
152 of 512 trials.

153 At the beginning of the experiment, participants were briefly familiarized with the task. They  
154 then performed 6 baseline, 50 adaptation and 4 washout blocks. The bimanual groups performed 6  
155 additional blocks – 5 re-adaptation and one additional washout block (see below). Each block consisted  
156 of 16 normal and 2 clamp trials. In total, participants performed at least 1080 trials. There were short  
157 breaks approximately every 200 trials and a 5 min break at the halfway point. Number and size of  
158 targets, timing, angles and force field strength were derived from the literature (e.g., Howard et al.,  
159 2012). At the end of the experiment, participants filled out pencil-paper questionnaires that asked them  
160 about potential strategies used in the experiment. In addition, we asked whether they had recognized  
161 a specific pattern between force field direction and cue position.

### 162 **Group 1: control, unimanual single reach**

163 We excluded and replaced two participants in the control group, because they had detected the rela-  
164 tionship between force field direction and position of targets and reported to have used this knowledge  
165 explicitly to move faster through the force field. The sample used for analysis was 20 (10 female, 10  
166 male,  $M_{age} = 26.55$ ,  $SD_{age} = 5.17$ ). We recorded EEG in the unimanual groups for another study,  
167 which is why the sample size was larger for unimanual than bimanual groups.

168 At the beginning of each trial, a white fixation cross on black background was displayed and the  
169 right arm of participants was moved to the middle target by the robot (see Figure 3D). This passive  
170 positioning took 1000 ms. Then, all targets (cue, middle & final) and the hand position cursor were



**Figure 3: Trial Design and experimental schedule.** A) Exemplary trial. Yellow dot - final target; grey dot - middle target(s); white dot - cue; red dot - hand position at the beginning of a trial; black arrow - desired reaching path during the trial; blue arrow - force field direction. In the bimanual groups the left hand reach was either performed actively, passively or only visually displayed. B) All cue final target combinations with arrows representing force field direction. For half of the participants the relationship between cue position and force field direction was the other way around. Yellow dot - final target; grey dot(s) - middle target(s); white dot with blue/orange border - cues; blue/orange arrow - force field direction. C) Experimental flow. re-adap. = re-adaptation. w. = washout. Phases with dashed lines are only executed in bimanual groups. D) Trial sequence. Reach to middle target was not (actively) performed in all groups.

171 displayed. After a random time drawn from a uniform distribution ranging from 1000 ms to 1400 ms,  
 172 the cue changed color from grey to white. This event was meaningful in the other experimental groups;  
 173 in contrast, control group participants were not instructed to do anything yet. After 600 ms the middle  
 174 target changed color from grey to white, which was the go-signal for participants to reach to the final  
 175 target. Once it was reached, feedback about the movement speed was displayed right above the middle  
 176 target. If the movement time from 2 cm away from the middle to the final target was in between  
 177 150 and 300 ms, feedback (in German) was 'good'; if it was outside this range 'too fast' or 'too slow',  
 178 respectively. The feedback was displayed for 600 ms. Finally, a white fixation cross was shown for 400  
 179 ms before the next passive positioning started for the next trial. When half the trials of a block were  
 180 completed the inter-trial-interval was 4 s instead of 400 ms.

181 Trials were immediately aborted and repeated within the same block when the cursor was not in the  
 182 middle target when the color changes of the targets took place. If participants left the middle target  
 183 earlier than 100 ms before or later than 500 ms after the go-signal, the trial was marked unsuccessful  
 184 and repeated at a random position within the current block. Timing, feedback and repetition criteria,  
 185 as introduced here, were the same for all groups.

186 For two participants in the control group the time between cue color change and middle target color  
 187 change was set to 400 ms instead of 600 ms. Performance of these two was similar to other participants  
 188 in the group and so we included them in our analysis.

189 **Group 2: active unimanual sequence**

190 There were 20 participants in the unimanual sequence group (10 female, 10 male,  $M_{age} = 25.9$ ,  
191  $SD_{age} = 4.45$ ). Unlike in the control group the hand of the participants was moved to the position of  
192 the cue and not the middle target during the passive positioning. The color change of the cue was the  
193 indicator for participants to move from the cue to the middle target. Participants were instructed to  
194 try to reach the middle target approximately when it changed color and subsequently reach from the  
195 middle to the final target. The aim was to perform two separate straight reaches but to pause in the  
196 middle target as short as possible. Feedback at the trial's end referred only to the movement time from  
197 middle to final target. Trials were aborted when the cursor was not in the cue when the first color  
198 change occurred and when the cursor left the middle target too early or too late (see control group).

199 Four participants had to perform faster cue-middle target reaches because the time between cue  
200 color change and target color change was only 400ms. Their performance was similar to that of other  
201 participants and so we included them in the data analysis.

202 **Group 3: active bimanual sequence**

203 The active bimanual sequence group comprised 8 participants (4 female, 4 male,  $M_{age} = 27.25$ ,  
204  $SD_{age} = 4.23$ ). Due to large effect sizes observed in prior research (Howard et al., 2012; Sheahan et al.,  
205 2016), we chose this sample size for all two hands groups. Although there was one more visual target  
206 in the two hand groups, timing of color changes was exactly the same as in the one-hand groups. The  
207 two middle targets changed color at the same time, 600ms after the cue color change.

208 At the beginning of a trial, the Kinarm robot moved both the right and the left arm; the left cursor  
209 to the cue position and the right cursor to the middle-right target. The color change of the cue was  
210 the signal for the participants to move the left arm to the middle-left target. Like in the unimanual  
211 sequence group, they were instructed to reach the middle-left target approximately when the middle  
212 targets changed color. The goal was to finish the left hand movement and subsequently reach with the  
213 right hand to the final target. To keep the trial abortion and repetition criteria consistent with the  
214 unimanual groups, participants had to have both cursors in their respective starting positions once the  
215 color change of the cue indicated the start of the left arm reach. Trials were also repeated when the  
216 right hand left the middle-right target more than 100ms too early or more than 500ms too late. Like in  
217 the unimanual sequence group, force fields and force channels (for clamp trials) were only ever present  
218 for the second reach, but never for the left hand. Feedback displayed after the movements was only  
219 about the right hand movement speed from the middle-right to the final position.

220 There were 6 additional blocks in the bimanual groups. After the last washout block, participants  
221 performed 5 blocks in an active bimanual sequence re-adaptation condition and subsequently one final  
222 active washout block. These blocks were identical to those of the first adaptation and washout phases.

223 **Group 4: passive bimanual sequence**

224 Our sample comprised 8 participants (4 female, 4 male,  $M_{age} = 25.25$ ,  $SD_{age} = 2.92$ ). We excluded



225 and replaced two participants because they employed explicit strategies, which they reported in our  
226 debriefing questionnaire.

227 Like in the active bimanual sequence group, the left arm was positioned at the cue and the right  
228 arm at the middle-right target at the beginning of a trial. However, participants did not see a cursor  
229 at the position of the left hand and they did not actively move their left arm during the three main  
230 phases of the experiment. Instead, participants were instructed to keep their left arm relaxed while the  
231 Kinarm moved the left hand from cue to middle-left target following a minimum jerk trajectory after  
232 the cue color change. This passive reach of the left arm started 100ms after the go-signal and took 550  
233 ms to mirror an average active reach and the preceding reaction time. Participants were instructed to  
234 start their right hand reach to the final target once they felt that the passive movement of the left hand  
235 finished. They were told that the color change of the middle targets did not always occur at the same  
236 time in relation to the passive left arm movement to discourage participants to discount the passive arm  
237 movement and only pay attention to the color change as a start signal. After the experiment, we asked  
238 participants whether they noticed that the end of the passive left arm movement always coincided with  
239 the middle targets color change and whether they had used this color change as a strategy to initiate  
240 their right arm reach. This was the case for one participants; we evaluate this point in the Discussion.

241 After the main three phases, participants performed five re-adaptation blocks and one washout block  
242 with the same instructions as the active bimanual sequence group. They experienced the same force  
243 field directions as in the adaptation phase; however, now they had to actively move the left hand. This  
244 post-test assessed whether there was any transfer of force field adaptation that may have taken place  
245 in the experiment's prior phases from passive to active left hand movement.

#### 246 **Group 5: visual bimanual sequence**

247 There were 8 participants in the visual bimanual sequence group (4 female, 4 male,  $M_{age} = 24$ ,  $SD_{age}$   
248  $= 2.73$ ). During the main 3 phases of the experiment, participants did not move their left arm. At  
249 the start of each trial, only the right hand was positioned to the middle-right target. Once the targets  
250 were displayed, there was, however, also a red cursor at the cue position. After the cue color change,  
251 this cursor moved to the middle-left target with the same motion dynamics as the passive movement in  
252 the passive bimanual sequence group. Participants were instructed to start their right hand reach once  
253 the red cursor reached the middle-left target. They were also asked not to use the middle target color  
254 changes as a go-signal but instead focus on the moving red cursor. Three participants paid attention  
255 to the color changes; we address this point in the Discussion.

256 Like the other bimanual groups, participants performed 6 blocks of active bimanual movements at  
257 the end of the experiment to assess learning transfer.

## 258 2.2 Data analysis

259 We pre-processed data in Matlab (R2021a). The Kinarm measured angles of the elbow and shoulder  
260 joints. We low-pass filtered this data with a cutoff at 10 Hz and added hand velocity, acceleration and  
261 commanded forces.

### 262 Maximal perpendicular error (MPE)

263 We performed our main analysis in Python (3.7) using the libraries numpy (Harris et al., 2020),  
264 pandas (McKinney et al., 2010), scipy (Virtanen et al., 2020), scikit-learn (Pedregosa et al., 2011), as  
265 well as matplotlib (Hunter, 2007) and seaborn (Waskom, 2021) for plotting. We excluded all aborted  
266 and repeated trials. Our first outcome measure was the maximal perpendicular error (MPE), defined as  
267 the signed maximal deviation in cm from the straight line between middle (-right) and final target of the  
268 right arm trajectory and reflected adaptation performance. A positive value denoted that participants  
269 had exhibited a curved trajectory in the direction of the force field. The MPE was defined between 2  
270 cm away from the midpoint of the middle target and the end of the final target. We excluded trials  
271 when it was obvious that participants had started the reach towards an incorrect target (13 across all  
272 samples).

### 273 Force field compensation (FFC)

274 Our second outcome measure was force field compensation (FFC) in clamp trials. To calculate  
275 FFC, we extracted force data within a 150 ms time window centered on the time of peak velocity. Next,  
276 we calculated the ideal force profile which would have counteracted the missing force field based on  
277 movement velocity. The measured force against the channel walls were linearly regressed on the ideal  
278 force profile with the intercept forced to zero. We defined FFC as the slope of the regression multiplied  
279 with 100%.

### 280 Statistical analysis

281 The focus of our study was on motor adaptation learning and differences in this aspect between  
282 groups. We quantified current motor adaptation performance with the MPE in normal trials and FFC  
283 in clamp trials. We averaged MPE and FFC over block and calculated the mean and standard error  
284 over participants for each group (see Figures 5A&B, 6A&B).

285 To measure the degree of adaptation each participant exhibited, we calculated three dependent  
286 variables. First, we subtracted the average MPE of the first adaptation block from the average of  
287 the last two adaptation blocks for each participant (MPE change adaptation). A negative MPE change  
288 adaptation value indicates that straighter reaches occurred at the end of the adaptation phase compared  
289 to the beginning. The more negative the value, the greater was the performance improvement. Second,  
290 we calculated the difference of the average MPE of the last baseline and first washout block (MPE  
291 change baseline/washout). A negative value means that a participant made systematically more curved  
292 reaches counteracting the experienced force fields in the washout block than in the baseline block.  
293 Consequently, the more negative the value, the bigger was the force field after-effect. This reaching

294 behavior indicates that participants adapted to the force field and exhibited after-effects when the force  
295 field was removed (e.g., Gandolfo, 1996). Third, we calculated the average FFC for each participant in  
296 the last four blocks in the adaptation phase (FFC final adaptation). A FFC final adaptation value of  
297 100% would indicate that participants perfectly adjusted their reaches to the force fields.

298 To answer our research questions, we performed planned comparisons between groups (see Figure  
299 2). To assess differences in motor adaptation due to a same or opposite arm prior movement, we  
300 compared all three dependent variables between the control, uni-, and bimanual active sequence groups  
301 (see Figure 3). For each group comparison we calculated the difference of the mean of the dependent  
302 variable. Next, we permuted group labels and computed the resulting means' difference. We repeated  
303 this 5000000 times or until the number of exact possible permutations was reached. The  $p$ -value was  
304 defined as the proportion of sampled permutations where the absolute difference was greater than  
305 the absolute observed difference. Following the same rationale, we compared all dependent variables  
306 within-group against zero (indicating no performance change) to assess whether group performance  
307 improved or worsened over time. For each family of permutation tests, we adjusted the  $p$ -value using  
308 the Bonferroni-Holm correction. We defined a family of tests as tests evaluating the same dependent  
309 measure (1 family = 11 tests).

310 To investigate whether sensory information in one modality of the opposite arm during the prior  
311 movement is sufficient for adaptation to occur, we compared performance measures between the three  
312 bimanual groups and within the groups. In addition, based on the observation that the learning curves  
313 of the active uni- and bimanual sequence groups differed, we investigated the slope of adaptation in  
314 both groups at the beginning of the adaptation phase (first 10 blocks) to identify potential learning  
315 differences at an early stage of the experiment. We performed a linear mixed effects analysis in R using  
316 `afex` (Singmann et al., 2016). We entered block number and group membership as well as the interaction  
317 term as fixed effects. As random effects, we included by-participant random slopes and intercepts. We  
318 employed the Kenward-Roger method to obtain  $p$ -values.

319 We used an explorative approach to examine performance in the re-adaptation phase in the bimanual  
320 sequence groups. We were interested to see if any transfer of learning occurred from a passive/visual to  
321 an active bimanual sequence. Due to the small number of blocks in the re-adaptation phase, we did not  
322 look at performance improvement within this phase but rather compared performance in this phase to  
323 performance at the end of adaptation. We averaged the MPE of the last five adaptation blocks of each  
324 participant and subtracted the average MPE of the re-adaptation phase (MPE re-/adaptation change).  
325 We again performed within and between permutation tests with this value.

326 To investigate to what extent the three measures, MPE change adaptation, MPE change base-  
327 line/washout and FFC final adaptation, reflect the same underlying factor, we calculated Pearson's  
328 correlation between two measures each across participants.

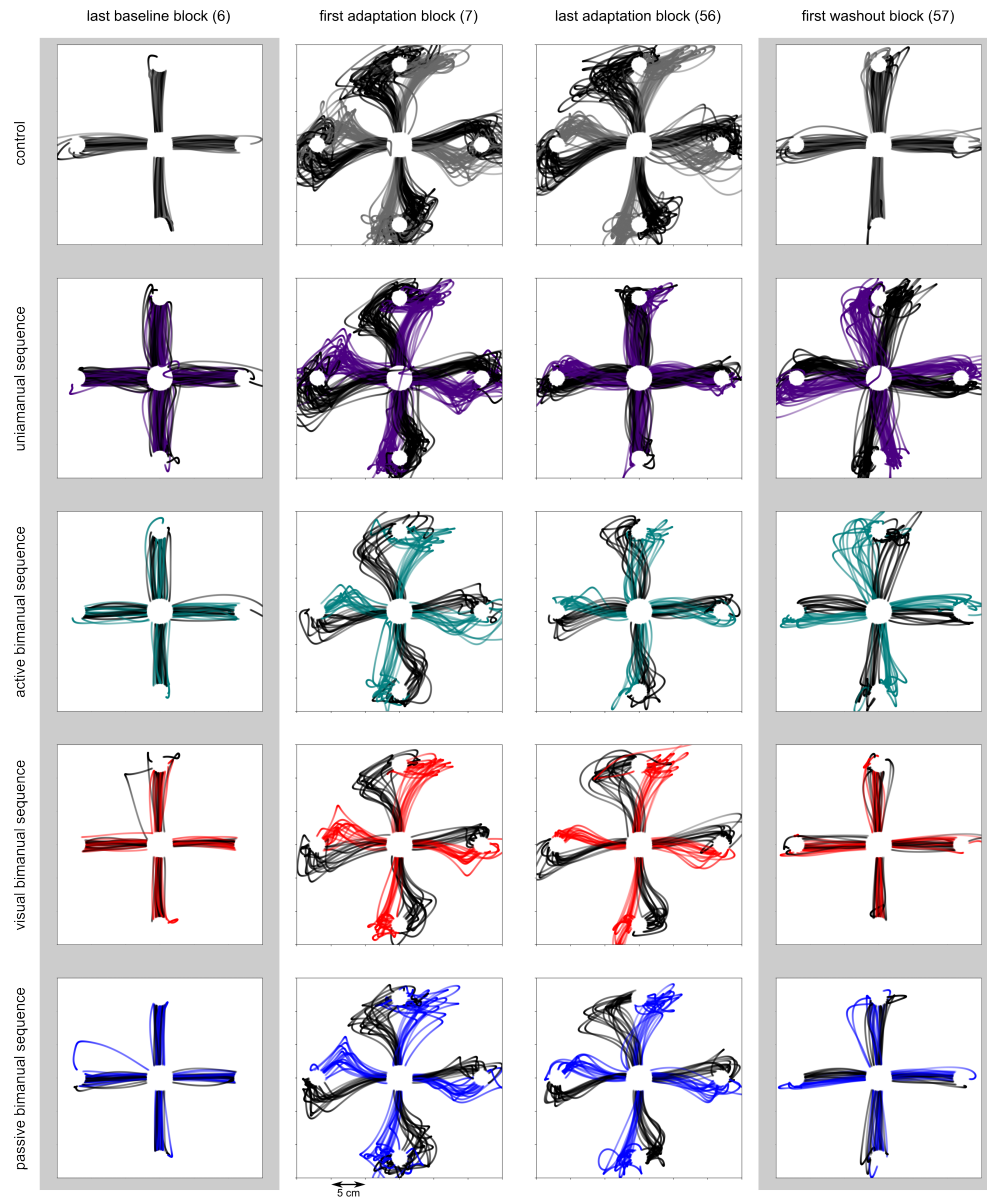


Figure 4: **Reaching trajectories.** Single trial trajectories of all participants in selected blocks of the experiment.

### 3 Results

All participants performed reaches from a middle position to final targets. Opposing force fields perturbed reaches during the (re-)adaptation phase of the experiment. Figure 4 depicts all trajectories from middle (-right) to final target of relevant blocks of all participants. At the end of the adaptation phase, participants in the active sequence groups made straighter reaches between the middle and final targets than at the beginning of adaptation, when the force field had just been introduced. Moreover, when the force field was removed, strong after-effects were evident as curving of reach trajectories in the direction of the former force fields, due to participants being prepared to counter the force field they had previously encountered. Adaptation and after-effects indicate that participants adapted their reaches to the respective force fields.

### 339 Unimanual groups vs. active bimanual sequence group.

340 First, we asked whether a prior movement with the opposite arm can be used as an effective cue  
341 for learning force field specific adaptation. In addition, we investigated the degree of adaptation in  
342 comparison to same arm prior movements as a cue. To this end, we compared MPE changes and FFC  
343 final adaptation to zero (no performance change) within the control, unimanual and bimanual sequence  
344 group as well as across groups.

345 For each participant, we subtracted the average MPE of the first adaptation block from the average  
346 of the last two adaptation blocks to obtain a measure of the MPE change during the adaptation  
347 phase. MPE change during the adaptation phase was not significant in the control group ( $p = 0.5887$ ;  
348 see Figure 5C). Control participants did not improve in counteracting the forces over the course of  
349 the adaptation phase. In contrast, performance of both the unimanual ( $p = 1.7e-05$ ) and the active  
350 bimanual sequence group ( $p = 0.0469$ ) improved over the adaptation phase. Improvement was greater  
351 in both sequence groups compared to the control group ( $p_{unimanual} < 1e-07$ ;  $p_{bimanual} = 3.2e-06$ ) and  
352 greater in the unimanual compared to the bimanual sequence group ( $p = 0.043$ ). These results imply  
353 that prior movements of the opposite arm can setup the sensorimotor system in a way that allows  
354 force field specific adaptation. After repeated exposure to interfering forces during reaching to a target,  
355 movement kinematics of the prior opposite arm movement seem to be represented together with specific  
356 motor actions which allow counteracting the forces. This linkage of two movements of two arms seems  
357 to be less strong than linkage between two movements of one arm.

358 In addition, we assessed MPE change from the baseline to the washout phase by subtracting the  
359 average MPE of the last baseline block from the first washout block. MPE baseline/washout changes  
360 were present in all groups ( $p_{control} = 0.003$ ;  $p_{unimanual} = 1.7e-05$ ;  $p_{bimanual} = 0.043$ ; see Figure 5D).  
361 This means that all groups showed some bias to curve their reaches in the direction from where the  
362 force field was coming from before. The changes were greater in the two sequence groups compared to  
363 the control group ( $p_{unimanual} < 1e-07$ ;  $p_{bimanual} = 3.2e-06$ ). There was no significant difference between  
364 the two sequence groups ( $p = 0.132$ ). These results demonstrate that movements of two arms can be  
365 linked.

366 To confirm our findings with a measure of feedforward adaptation, we calculated FFC final adapta-  
367 tion by averaging forces measured in clamp trials in the last four blocks in the adaptation phase. FFC  
368 comparisons revealed the same pattern as MPE changes in the adaptation phase: FFC final adaptation  
369 was different from zero in both sequence groups but not in the control group ( $p_{unimanual} = 1.7e-05$ ;  
370  $p_{bimanual} = 0.043$ ;  $p_{control} = 0.080$ ; see Figure 5E). Stronger adaptation was observed in both sequence  
371 groups compared to the control group ( $p_{unimanual} = 0$ ;  $p_{bimanual} = 6.4e-06$ ). Finally, the unimanual  
372 sequence group compensated more over the course of the adaptation phase than the bimanual sequence  
373 group ( $p = 0.032$ ). In sum, the result patterns are consistent with the notion that prior movement kine-  
374 matics of the opposite arm can indeed serve as effective cues for force field specific motor adaptation.

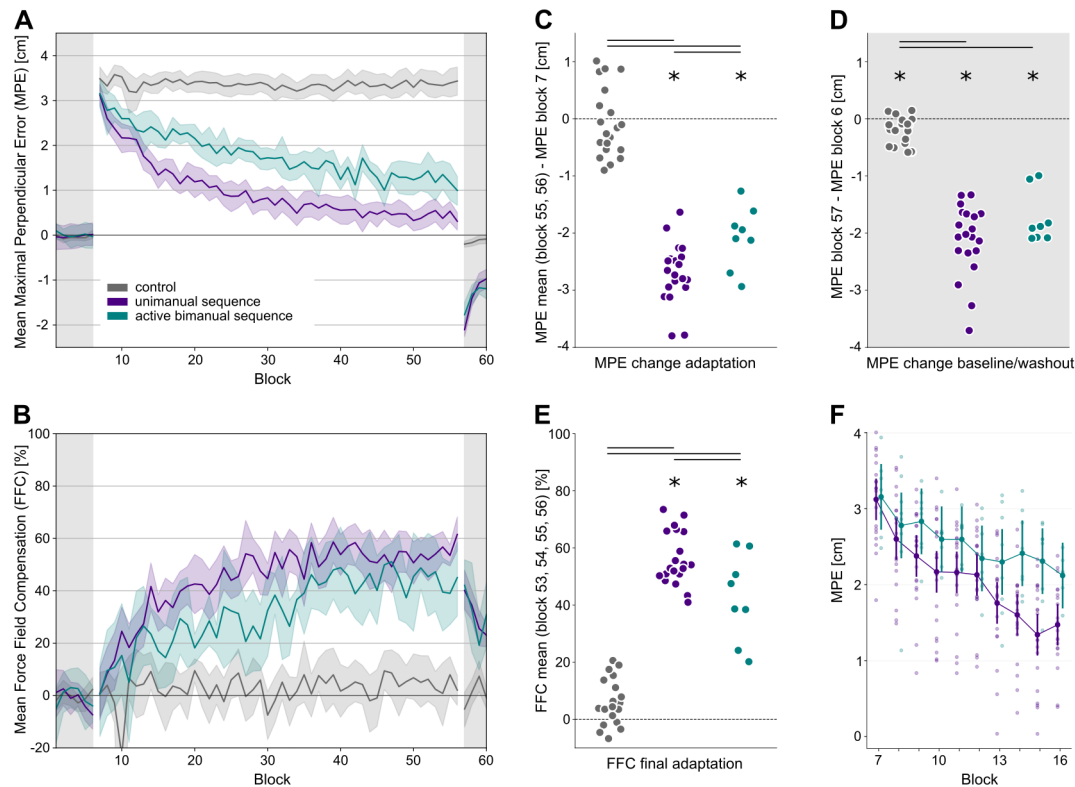


Figure 5: **Unimanual groups vs. active bimanual sequence group.** A) MPE averaged over participants and trials within one block. Force fields were present from block 7 to block 56 (white background). Error bands depict SEs across participants. B) FFC averaged over participants and trials within one block. C) Each dot depicts the difference between average performance in the first and last two adaptation blocks of one participant. Lines denote significant differences between groups  $p < .05$ . Stars mark significant within group effects  $p < .05$ . D) MPE differences between the first washout and the last baseline block. E) Average FFC in the last 4 adaptation blocks. F) MPE in the first 10 adaptation blocks; each small dot depicts average performance per block of one participant; larger dots display group averages; error bars depict 95% confidence intervals.

375 Yet, two of three dependent measures indicate that final adaptation is stronger in the uni- compared  
 376 to the bimanual group.

377 To investigate whether this difference in adaptation occurs during early learning in the adaptation  
 378 phase we performed a mixed model with the between groups factor group (uni- vs. bimanual sequence)  
 379 and within group factor block (block 7-16). We found main effects for group ( $F_{1,26} = 4.65, p = .040$ )  
 380 and block ( $F_{9,234} = 37.87, p < .001$ ) as well as an interaction between group and block ( $F_{9,234} = 4.39, p$   
 381  $< .001$ ; see Figure 5F). Participants in the unimanual sequence group had a steeper learning curve than  
 382 participants in the bimanual sequence group during early learning. This result indicates that linking of  
 383 movements over body parts might be slower than linking movements within one body part.

#### 384 **Active vs. visual vs. passive bimanual sequence group.**

385 To investigate whether the perception of specific opposite arm movements without active execution  
 386 allows motor adaptation, we tested for effects of adaptation (MPE changes and FFC final adaptation)  
 387 in each group separately as well as across groups. MPE changes in the adaptation phase were neither  
 388 significant for the visual ( $p = 0.0625$ ) nor the passive ( $p = 0.0703$ ) bimanual sequence group (see Figure

389 6C). Moreover, the active group improved their performance to a greater extent than the visual ( $p =$   
390 0.0012) and the passive ( $p = 0.0022$ ) group. Finally, the change in performance was not different  
391 between the visual and passive group ( $p = 0.8382$ ). These results suggest that perception of movement  
392 in one sensory modality, in the absence of active movement, does not sufficiently allow force field specific  
393 adaptation.

394 However, MPE changes from the baseline to the washout phase were evident in all groups ( $p_{visual} =$   
395 0.0430;  $p_{passive} = 0.0469$ ; see Figure 6D). This indicates that some learning does occur in the sensory  
396 groups even though it is not evident in the adaptation phase. The changes were greater in the active  
397 compared to the visual ( $p = 0.0012$ ) and passive ( $p = 0.0044$ ) groups, highlighting that sensory infor-  
398 mation of the opposite arm can not be used as a substitute for active movement in this paradigm. No  
399 difference was observed between the visual and the passive group ( $p = 0.1032$ ).

400 The overall result pattern was equivalent for FFC final adaptation (see Figure 6E). All groups showed  
401 some compensation ( $p_{visual} = 0.0430$ ;  $p_{passive} = 0.0469$ ), but it was stronger in the active compared to  
402 the visual ( $p = 0.0076$ ) and the passive ( $p = 0.0025$ ) group. The visual and passive groups did not differ  
403 in their FFC final adaptation ( $p = 0.6706$ ). In total, these results confirm that movement directions of  
404 visual or passive prior movement with the other arm are not easily linked with motor actions needed to  
405 counteract a specific force field. Information about visual or passive movement kinematics of another  
406 limb might not be readily utilized to adjust movement plans.

#### 407 **Transfer.**

408 Finally, we asked whether the hidden learning in the visual/passive conditions could be transferred  
409 to an actively performed two arm motor sequence. To this end we compared the MPE from the end  
410 of adaptation to the MPE during the re-adaptation phase. We observed performance changes in the  
411 passive ( $p = 0.0273$ ) and active ( $p = 0.0273$ ) bimanual sequence groups, but not in the visual group ( $p$   
412  $= 0.1563$ ; see Figure 6F). Participants in the active bimanual sequence group performed worse during  
413 the re-adaptation phase than at the end of the adaptation phase. This result is likely caused by the  
414 washout phase in between the adaptation and re-adaptation phase, in which participants re-adapted to  
415 an environment without force fields. Participants in the passive group, however, were able to reduce their  
416 MPE in the re-adaptation blocks compared to the last adaptation blocks. It is an open question whether  
417 this result is due to a motor learning mechanism or due to the need of the participants to stabilize their  
418 arm movements more when both arms have to be actively controlled. Comparisons between groups  
419 revealed a difference in MPE re-/adaptation change between the active and visual group ( $p = 0.0039$ )  
420 as well as between the active and passive group ( $p = 0.0009$ ). The MPE was not different between the  
421 visual and passive groups ( $p = 0.1414$ ). Overall, the transfer results further support the conclusion that  
422 initial learning was limited in the visual and passive group, making it difficult for transfer of learning  
423 to occur.

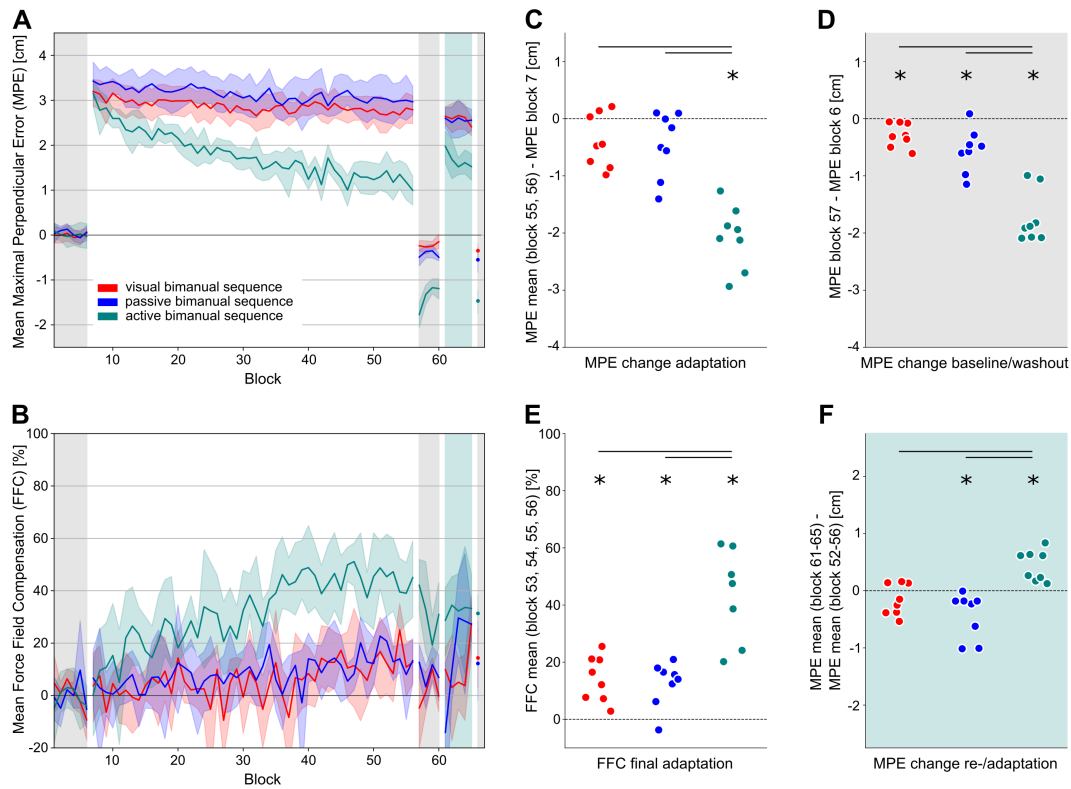


Figure 6: **Active vs. visual vs. passive bimanual sequence group.** A) MPE averaged over participants and trials within one block. Force fields were present from block 7 to block 56 (white background) and block 61 to block 65 (green background). All participants performed an active bimanual sequence in blocks 61 to 66. Error bands depict SEs across participants. B) FFC averaged over participants and trials within one block. C) Each dot depicts the difference between average performance in the first and last two adaptation blocks of one participant. Lines denote significant differences between groups  $p < .05$ . Stars mark significant within group effects  $p < .05$ . D) MPE differences between the first washout and the last baseline block. E) Average FFC in the last 4 adaptation phase. F) MPE differences between the re-adaptation phase and the last 5 blocks of the adaptation phase.



424 **Correlation between measures.**

425 In order to investigate whether dynamics were similar across our different measures, we calculated  
426 a correlation between them. All correlations between MPE change adaptation, MPE change base-  
427 line/washout and FFC final adaptation across participants were high and in the expected direction (see  
428 table 1), suggesting that all variables measured the same underlying construct.

Table 1: **Correlations between measures.** Pearson's r correlations between dependent variables.

	MPE change adaptation	MPE change baseline/washout
MPE change baseline/washout	0.8381	
FFC final adaptation	-0.8485	-0.7881

429 **4 Discussion**

430 Fine-tuning movements to reduce discrepancies between motor command and sensory feedback is a key  
431 mechanism of motor learning. In this study, we investigated whether linking sequential movements of  
432 two arms can support motor adaptation to opposing force fields. We report two main findings. First,  
433 we found that prior movements of the opposite-arm enabled adaptation to opposing force fields. This  
434 finding demonstrates that learning of a movement can be influenced by a linked movement of the other  
435 arm. Specifically, if there are consistent relations between kinematics of different arm movements in  
436 a motion sequence, the motor system can take advantage of this information to adjust movements ac-  
437 cordingly. Second, visual and proprioceptive opposite-arm signals in the absence of an active movement  
438 were significantly less effective than active reaches, highlighting that actively using both arms is a key  
439 requirement in linking sequential, bimanual movements. In addition, we replicated previous findings  
440 showing that active same-arm prior movements facilitate adaptation, whereas stationary visual cues,  
441 though indicative of force field direction, do not (e.g., [Howard et al., 2012](#)).

442 **Unimanual vs bimanual sequence learning.**

443 Our findings indicate that formation of separate motor memories in a force field interference task is  
444 not only possible when distinct perturbations are encountered in unimanual movement sequences, but  
445 also in active, bimanual movement sequences. Notably, the bimanual movement chains were less effective  
446 than unimanual chains, evident in both, the smaller reduction of trajectory curvature as measured with  
447 the MPE in the adaptation phase and smaller forces applied against the expected perturbation as  
448 indicated by the FFC measure. Furthermore, comparison of the adaptation curves for unimanual and  
449 bimanual sequences during early learning indicated that adaptation in the bimanual context was not  
450 only weaker but also slower than in the unimanual context. Thus, chained movements of a single limb  
451 seem to be more readily linked and represented together than movements across limbs. Several factors  
452 may explain this difference.

453 First, if single movement elements of a sequence are difficult to perform, it is more likely that they  
454 are represented separately as discrete actions (Rand and Stelmach, 2000). This is also reflected by  
455 an increased response time when alternating between different hands in bimanual serial reaction time  
456 tasks (Bhakuni and Mutha, 2015; Trapp et al., 2012). Using different limbs within one sequence adds  
457 complexity, requiring more coordination and attention to execute the movement sequence according to  
458 the movement plan (Gálvez-García et al., 2014). The increased difficulty might inhibit the linking of  
459 bimanual sequences (Kennedy et al., 2021). As a result, movements might be preferentially represented  
460 discretely.

461 Second, linking the movements of two different body parts might be harder due to the organization  
462 and structure of the brain. Neural patterns pertaining to a bimanual movement sequence are spread out  
463 over both hemispheres due to the lateralisation of the motor cortex (Gerloff and Andres, 2002). Thus,  
464 a wider and bihemispheric network of brain modules is involved in bimanual compared to unimanual  
465 movement sequences, which might, accordingly, be more difficult to establish and maintain (Noble et al.,  
466 2014).

467 Third, neural crosstalk might interfere with learning of bimanual tasks (Kennedy et al., 2021; Swin-  
468 nen, 2002). Neural crosstalk occurs during bimanual movements when neural signals designated to  
469 muscles in one arm are also sent to homologous muscles in the other arm (Cardoso de Oliveira, 2002).  
470 Interference emerges when additional, conflicting signals are received in close temporal proximity. In  
471 our active bimanual sequence group, left and right hand reaches had to be made directly following one  
472 another; thus the related neural signals may have resulted in interference, hampering adaptation.

### 473 **Sensory information as a substitute for active movement in sequence learning.**

474 In our study, providing prior visual or proprioceptive feedback of the opposite-arm movement did  
475 not enhance adaptation of the moving arm. This suggests that sensory information on its own does not  
476 provide a substitute for active movement in bimanual sequence learning. This finding contrasts with  
477 prior research in which visual and passive prior same-arm movements were effective cues for adaptation  
478 to opposing force fields (Howard et al., 2012). The contrast could be explained by sensory information  
479 of the same limb being weighted differently than information of another limb during sensorimotor  
480 integration processes. Sensorimotor integration is the ability to extract relevant sensory inputs to  
481 create informed motor outputs (Wolpert et al., 1995). Sensory information received from a same-arm  
482 visual or passive "movement" directly affects the state estimation of the arm and thus the internal  
483 model and motor command of the next reach, allowing force field specific adaption. Sensory changes  
484 in another limb, however, do not bear the same relevance for the execution of a reach and may not  
485 be integrated computationally within a bimanual motor sequence. In addition, in the visual bimanual  
486 sequence group, participants may not have represented the red cursor as their left arm. In line with  
487 this explanation, visual cues which cannot be directly related to the state of the moving arm have  
488 not lead to adaptation in previous research, for instance, spatially static visual cues or field-specific

489 cursor/background colors (Cothros et al., 2009; Howard et al., 2012, 2013).

490 Even though active engagement seems to be necessary for strong linking to occur across arms, some  
491 participants in the visual and passive bimanual sequence group were able to reduce their movement error  
492 over the course of the adaptation phase, indicating that inter-individual differences exist in whether and  
493 how cues can be used for motor adaptation. One factor that could influence individual adaptation is  
494 the attention given to the perceptual information of the opposite-arm. However, in our debriefing, four  
495 participants indicated that they had primarily attended to the color switch of the middle targets, rather  
496 than anticipating the end of the visual or proprioceptive left hand movement. Despite this strategy,  
497 these participants' performance was not appreciably different from that of other participants. Thus,  
498 which factors may drive the adaptation differences between participants remains unclear.

499 In addition, we asked whether participants could transfer any learning obtained in a setting where  
500 the prior movement was only visual or passive to an active bimanual movement. This question was  
501 motivated by sports and rehabilitation practices, where a similar transfer would be highly desirable  
502 to support motor learning processes. In our experiment, however, learning was, for the most part,  
503 absent when only visual or passive-proprioceptive information of the prior opposite-arm movement  
504 were available. A transfer of overt improved performance to an active bimanual sequence was therefore  
505 impossible.

506 Surprisingly, there was immediate improvement in performance in the passive bimanual sequence  
507 group once they actively performed the task. The reduction of the MPE in the re-adaptation phase  
508 could, however, originate not from force field specific adaptation but from increased muscle co-contraction  
509 in the right arm. The increased stiffness would result in smaller MPEs without true learning of the  
510 force fields. Co-contraction of the right arm might be more pronounced in the re-adaptation than the  
511 adaptation phase because participants had to control their left arm movement in addition to their right  
512 arm during the active re-adaptation. Taken together, we cannot draw strong conclusions about transfer  
513 ability from linked sensory/active movements to active motor sequences.

#### 514 **Motor adaptation vs. sequence learning.**

515 Motor theories usually distinguish between motor adaptation and skill learning. Motor adaptation  
516 entails a trial-by-trial change evoked by a mismatch between expected and received feedback and is  
517 thus a recalibration process (Wolpert et al., 2011). In contrast, skill learning entails the creation of a  
518 new movement pattern (Diedrichsen and Kornysheva, 2015). It is currently unknown whether findings  
519 about motor adaptation generalize to motor skill learning. In our view, it is crucial for complex bilateral  
520 motor behavior and learning to adjust part of a movement sequence according to kinematic parameters  
521 of the same sequence; this appears to us to be equivalent in multi-limb adaptation and skill learning.  
522 Our present results suggest, for example, that a novice juggler will improve over time by utilizing  
523 kinematic information from one arm to adjust movements of the other more and more. Bimanual tasks  
524 with concurrent movements of the arms have already shown that internal models of arm movements

525 encompass not only kinematic information about the relevant arm but also about the opposite-arm to  
526 allow smooth compensation and flexible interaction between them (Yokoi et al., 2011). In our study,  
527 we provide first evidence that the selection process of internal models is influenced by prior movements  
528 of another limb and thereby contribute to a mechanistic understanding of complex bilateral motor  
529 behavior. Our finding is relevant for motor learning in both rehabilitation and sport settings. For  
530 example, in rehabilitation of stroke, activating a specific motor memory of the affected hand (e.g.,  
531 reaching for a cup) could be cued and facilitated by a prior opposite-arm movement. Similarly, in  
532 sports, deliberately using movement sequences to differentiate between otherwise interfering moves  
533 (e.g., twisting once or twice in gymnastics) could be especially beneficial. These exciting prospects  
534 await future research.

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