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1 Individual movement features during prism adaptation

2 correlate with after-effects and interlimb transfer

3  
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25 **Abstract**

26 The human nervous system displays such plasticity that we can adapt our motor behavior to  
27 various changes in environmental or body properties. However, how sensorimotor adaptation  
28 generalizes to new situations and new effectors, and which factors influence the underlying  
29 mechanisms, remains unclear. Here we tested the general hypothesis that differences across  
30 participants can be exploited to uncover what drives interlimb transfer. Twenty healthy adults  
31 adapted to prismatic glasses while reaching to visual targets with their dominant arm. Classic  
32 adaptation and generalization across movement directions were observed but transfer to the  
33 non-dominant arm was not significant and inter-individual differences were substantial.  
34 Interlimb transfer resulted for some participants in a directional shift of non-dominant arm  
35 movements that was consistent with an encoding of visuomotor adaptation in extrinsic  
36 coordinates. For some other participants, transfer was consistent with an intrinsic coordinate  
37 system. Simple and multiple regression analyses showed that a few kinematic parameters  
38 such as peak acceleration (or peak velocity) and variability of movement direction were  
39 correlated with interlimb transfer. Low peak acceleration and low variability were related to  
40 extrinsic transfer while high peak acceleration and high variability were related to intrinsic  
41 transfer. Motor variability was also positively correlated with the magnitude of the after-effect  
42 systematically observed on the dominant arm. Overall, these findings on unconstrained  
43 movements support the idea that individual movement features could be linked to the  
44 sensorimotor adaptation and its generalization. The study also suggests that distinct  
45 movement characteristics may be related to different coordinate frames of action  
46 representations in the nervous system.

47 **Introduction**

48 Whenever we learn something, we often would like it to generalize to other conditions: for  
49 instance, we may hope that learning tennis will also result in improvements in table tennis and  
50 squash. However, the sensorimotor system needs some specificity, so that each action is  
51 optimal in its own context. Some skills in tennis, such as prediction of ball bouncing, should  
52 thus not be generalized to other contexts such as squash. In the present study, we probed the  
53 generalization of sensorimotor adaptation by assessing how adapting to a new visuomanual  
54 relationship transfers across effectors.

55         Research on the transfer of short-term adaptation between the arms revealed the  
56 existence of two motor representations in the human nervous system: an effector-specific  
57 representation and an effector-independent representation (Wang & Sainburg 2003; Morton &  
58 Bastian 2004; Vangheluwe et al. 2006; Taylor et al. 2011; Joiner et al. 2013; Mostafa et al.  
59 2014). Such effector-independent representation would underlie the interlimb transfer of  
60 sensorimotor adaptation, which also appears to be shaped by contextual conditions (Krakauer  
61 et al. 2006) and the cause of motor errors (Berniker & Kording 2008). Generalization is also  
62 likely influenced by the kinematic properties of movements, as sensorimotor adaptation was  
63 found to generalize across movement speeds to a certain limit (Kitazawa et al. 1997). Indeed,  
64 Kitazawa et al. (1997) showed that when movements performed during prism adaptation were  
65 fast, the after-effect was greater when movements in the generalization phase were also fast  
66 compared to when movements were slower. In fact, this study showed that prism adaptation  
67 was not entirely specific to movement speed but also that any difference between the training  
68 conditions and the test condition could limit generalization, with the greater the difference,  
69 the smaller the generalization. It has also been suggested that motor variability is linked to the  
70 adaptation process (Wu et al. 2014). Wu et al. (2014) reported that higher task-relevant motor  
71 variability during baseline was correlated with faster adaptation. But as a recent meta-analysis

72 (He et al. 2016) did not confirm this correlation between motor variability and adaptation rate,  
73 it is currently hypothesized that motor variability may in part reflect active exploration of  
74 movement parameter space in order to optimize sensorimotor adaptation (Pekny et al. 2015;  
75 Therrien et al. 2016). Despite the body of work on these issues, the factors and mechanisms  
76 modulating generalization of sensorimotor adaptation remain unclear. Here we tested the  
77 hypothesis that specific kinematic characteristics of movements may be linked to the  
78 interlimb transfer of sensorimotor adaptation.

79 Lefumat et al. (2015) reported substantial individual differences in interlimb transfer  
80 of force-field adaptation but also showed that transfer can be qualitatively and quantitatively  
81 described for each young individual based on motor variability and velocity during  
82 adaptation. Based on these data, Lefumat et al. (2016) could predict the transfer of older,  
83 neurological patients suffering from a massive proprioceptive deafferentation. Considering  
84 these studies and others (Wu et al. 2014; Therrien et al. 2016), we tested in the present study  
85 the hypothesis that movement variability is linked to interlimb transfer based on another  
86 classic adaptation paradigm, the prism adaptation paradigm (Harris 1963; Held & Freedman  
87 1963; Redding & Wallace 1988; Martin et al. 1996; Kitazawa et al. 1997; O'Shea et al. 2014).  
88 The previous findings on interlimb transfer of force-field adaptation may not apply to the  
89 interlimb transfer of visuomotor adaptation because distinct neural mechanisms appear to  
90 underlie adaptation to new visuomotor mappings (using a visuomotor rotation or prismatic  
91 glasses for instance) and adaptation to new limb dynamics (Haith & Vijayakumar 2009;  
92 Donchin et al. 2012). Given these differences, we hypothesized that the factors which  
93 correlate with the interlimb transfer of prism adaptation would differ from those identified in  
94 previous studies on adaptation to a velocity-dependent force field (Lefumat et al. 2015). More  
95 specifically, we expected movement variability to influence the interlimb transfer of prism  
96 adaptation more than movement velocity.

97           To facilitate the comparison between prismatic and force-field adaptation, we used the  
98 protocol and setup of Lefumat et al. (2015) but with a prismatic instead of dynamic  
99 perturbation. Although interlimb transfer of prism adaptation has sometimes been found to be  
100 non-significant (Kitazawa et al. 1997; Martin et al. 1996; Michel et al. 2007), we  
101 hypothesized based on several previous studies (Harris 1963; Cohen 1967; Cohen 1973; Taub  
102 & Goldberg 1973; Choe & Welch 1974; Wallace & Redding 1979) that interlimb transfer  
103 would be observed in the form of an after-effect on the first movement made after prismatic  
104 adaptation, without prisms, with the opposite, non-exposed arm. We reasoned that the  
105 presence of an after-effect would indicate the presence of interlimb transfer, but also that the  
106 direction of the after-effect would allow us to determine whether visuomotor adaptation is  
107 encoded in extrinsic or intrinsic coordinates (Criscimagna-Hemminger et al. 2003; Carroll et  
108 al. 2014; Stockinger et al. 2015). Specifically, when using prisms displacing the visual field  
109 rightward, encoding of dominant-arm adaptation in extrinsic coordinates (associated with a  
110 leftward compensation) would predict a leftward after-effect on the non-dominant arm. In  
111 contrast, encoding in intrinsic coordinates (associated with shoulder and elbow abduction for  
112 instance) would predict a rightward after-effect. Lastly, because the degree of handedness has  
113 been shown to affect motor control and interlimb transfer (Chase & Seidler 2008; Sainburg  
114 2014; Lefumat et al. 2015), we tested a mixed set of right- and left-handers in order to provide  
115 a general model of interlimb transfer of prism adaptation.  
116

## 117 **Methods**

### 118 *Participants*

119 Twenty young adults (thirteen men, seven women, mean age:  $23.5 \pm 2.7$  years) participated in  
120 the experiment. None of the participants declared a sensorimotor or a neurological deficit.  
121 Participants had normal vision or corrected-to-normal vision with contact lenses. Handedness  
122 was assessed with the 10-item version of the Edinburgh inventory (Oldfield 1971). Eight  
123 participants with a laterality quotient (LQ) between -100% and -10% were classified 'left  
124 handed' and twelve participants were classified 'right handed' (LQ between +60% to  
125 +100%).

126 Participants gave their written informed consent prior to the study, which was  
127 approved by the institutional review board of the Institute of Movement Sciences and was  
128 performed in accordance with the standards of the Declaration of Helsinki (1964).  
129 Participants were naive to the purpose of the experiment and were informed that they could  
130 stop the experiment at any moment.

131

### 132 *Experimental setup*

133 Seated participants were asked to reach toward flashed visual targets. On a horizontal board,  
134 at waist level, a visuo-tactile landmark (a circular hole of 2 cm in diameter) indicated the  
135 starting hand position. Visual targets were red light-emitting diodes (3 mm in diameter).  
136 Figure 1 shows that three targets were positioned on a 37-cm radius circular array at 0 deg.  
137 (straight-ahead), +20 deg. (to the right) and -20 deg. (to the left) with respect to start position.

138 For the entire experiment, participants viewed the set-up and their arm binocularly  
139 through specific goggles which allowed vision only through the prism lenses (O'Shea et al.  
140 2014). One set of goggles was standard (control) and the other was equipped with Fresnel 3M  
141 Press-on plastic lenses (3M Health Care, Specialties Division, St Paul, Minn., USA) as in

142 Martin et al. (1996). The 30-diopter (~17 deg.) lenses were mounted base-left (thus producing  
143 a rightward deviation of the visual field).

144 Infrared active markers were taped to the right and left index fingertips, whose  
145 positions were sampled at 350 Hz using an optical motion tracking system (Codamotion cx1  
146 and MiniHub, Charnwood Dynamics Ltd, Leicestershire, UK). The experimenter controlled  
147 the tracking system and the presentation of the visual targets from an adjacent room by using  
148 a customized software (Docometre) governing a real-time acquisition system (ADwin-Pro,  
149 Jäger, Lorsch, Germany).



150

151 *Figure 1: Experimental conditions, illustrated with a right-handed participant. During the*  
152 *PRE-exposure phase, participants reached toward one of three visual targets with the*  
153 *dominant and the non-dominant arms. During the exposure phase, participants reached*  
154 *toward the central target with the dominant arm while wearing prisms. During the POST-*  
155 *exposure phase, participants reached toward one of three targets with the non-dominant arm*  
156 *and then with the dominant arm. (Color not required for printed version).*

157

158



159 *Experimental procedure*

160 At the beginning of each trial, participants had to actively position their specified (left or  
161 right) hand at the starting location (Figure 1). They were asked to reach as fast and accurately  
162 as possible with their index finger toward the visual target, which was illuminated for 0.3 s.  
163 Participants were also instructed to 'reach in one movement' and not to correct their position  
164 after their finger contacted the horizontal board. No instructions were given with respect to  
165 hand path. 1.6 s after trial onset, a 100-ms tone informed the participant to go back slowly to  
166 the starting location. 7.4 s after trial onset, a 600-ms tone signalled to the participant that the  
167 trial had ended and that the next trial would start immediately. All participants were  
168 familiarized with the task during a preliminary phase.

169 To assess the interlimb transfer of sensorimotor adaptation, we employed a procedure  
170 inspired by DiZio and Lackner (1995) and Martin et al. (1996) in order to compare non-  
171 dominant arm performance just before and just after dominant arm performance with prisms.  
172 The experimental session consisted of 3 phases, illustrated on Figure 1:

- 173 – PRE-exposure phase (baseline): Participants executed 30 reaching movements with the  
174 dominant arm (DA) then 30 with the non-dominant arm (NDA) toward one of the three  
175 possible targets (10 trials per target for each hand). Trials toward the different targets were  
176 presented in a pseudorandom order which was similar for all 20 participants. When the  
177 PRE-adaptation phase was over, a 2-min break was given, goggles were removed and the  
178 control goggles previously worn by participants were discretely replaced with prismatic  
179 glasses. During the break, participants had to keep their eyes closed and stay motionless.
- 180 – Prism exposure phase: Participants performed 100 movements with the dominant arm  
181 (DA) toward the central target (0 deg.) while wearing the prisms deviating the visual field  
182 by ~17 deg. to the right. At the end of this phase, a second 2-min break was given and  
183 prisms were replaced with control goggles by the experimenter. During the break,

184 participants kept their eyes closed and stayed motionless.  
185 – POST-exposure phase: Participants first executed 30 reaching movements with the non-  
186 exposed non-dominant arm (NDA), and then 30 movements with the dominant arm (DA)  
187 (10 trials per target for each hand). For both blocks, the first presented target was the  
188 central target (then target order was pseudo-randomised). For the NDA block, the second  
189 target presented was the right target and the third target was the left target. For the DA  
190 block, the second target presented was the left target and the third target was the right  
191 target.

192 Participants were instructed not to move their opposite arm during or between trials.  
193 An infra-red camera allowed continuous monitoring of participant's behaviour. The head was  
194 unrestrained because stabilizing the head has been shown to preclude interlimb transfer of  
195 prism adaptation (Hamilton 1964). The Prism exposure phase lasted approximately 20 min,  
196 the complete reaching task lasting approximately 45 min.

197 Because previous work suggested that interlimb transfer depends on the perceived  
198 source of motor errors (the credit-assignment issue; Berniker and Kording 2008), we aimed at  
199 directly assessing the assignment of motor errors and determine whether it could influence  
200 interlimb transfer. Immediately after the end of the reaching session, participants were asked  
201 open questions to determine whether they consciously perceived errors in movement  
202 trajectory during the first trials of the exposure phase. Then we showed a top view of each  
203 participant's arm trajectory in the first trial of the exposure phase and asked participants to fill  
204 a questionnaire. Participants were thus asked, in a counterbalanced order, 'Did you associate  
205 the errors you made early in the exposure phase to external factors?' and 'Did you associate  
206 the errors you made in the exposure phase to yourself (e.g., internal factors such as fatigue,  
207 inattention...)?'. Participants answered these two questions by placing a mark on a 10-cm  
208 scale. The left extremity (0) of the scale indicated 'Do not agree at all' and the other extremity

209 (10) indicated ‘Strongly agree’. Finally, participants had to estimate whether errors were  
210 mostly associated with ‘Internal factors’ or ‘External factors’ by placing a mark on the scale  
211 with ‘Internal factors’ on the left extremity of the scale and ‘External factors’ on the other  
212 extremity.

213  
214 *Kinematic data analysis*

215 Data, which are available upon request, were analysed using Matlab (Mathworks, Natick,  
216 MA, USA). A few trials (0.9%) had to be discarded because they were not properly  
217 performed by the participants or were corrupted by noise. Position data from the markers on  
218 the right and left index fingertips were low-pass filtered with a dual-pass, no-lag Butterworth  
219 (cut-off frequency: 8 Hz; order: 2). Movement onset was defined as the first-time hand  
220 velocity reached 3 cm/s and movement offset as the first-time hand velocity dropped below 3  
221 cm/s. Given that prisms mostly influence the direction of arm reaching movements, final  
222 movement accuracy was computed as the angle between the vector from the start position to  
223 the target position and the vector from the start position to the hand position at movement  
224 offset. Initial movement direction was computed as the angle between the vector from the  
225 start position to the target position and the vector from the start position to the hand position  
226 at peak velocity (Wang & Sainburg 2003). Since peak velocity occurred around 150 ms after  
227 movement onset in the present study, initial direction was considered the most critical  
228 dependant variable because it mostly reflects the initial motor plan, before online visual  
229 feedback can substantially influence movement direction (Reichenbach et al. 2014; Sarlegna  
230 & Mutha 2015).

231  
232 *Statistical analysis*

233 Using Statistica 8 (StatSoft, Tulsa, OK, USA), repeated-measures analyses of variances  
234 (ANOVA) and t-tests allowed us to assess the significance of the results. First, to assess

235 adaptation of the DA, the mean data of the 10 movements toward the central target of the  
236 PRE-exposure phase (baseline) were compared with i) the first trials and the last trial of the  
237 Prism exposure phase (to analyse the effect of the visual perturbation induced by prisms and  
238 the adaptation) and ii) the first trial of the POST-exposure phase (to analyse the after-effect).  
239 The number of trials to adapt was computed by comparing for each participant a 95%  
240 confidence interval of initial direction during the baseline PRE-exposure phase to the initial  
241 direction of the first movements made during the Exposure phase. We determined the number  
242 of trials which were necessary for initial direction during the Exposure phase to fall back  
243 within the baseline's confidence interval. The after-effect value found on the DA of each  
244 participant was defined as the initial direction of the 1<sup>st</sup> trial made during the POST-exposure  
245 DA phase minus the mean of the initial direction of 10 trials made toward the central target  
246 during the PRE-exposure DA phase. We also assessed whether adaptation of DA movements  
247 toward the central target generalized across movement directions by comparing the mean data  
248 of the PRE-exposure movements toward one of the lateral targets to the value of the first trial  
249 in POST-exposure for the corresponding target.

250 To assess interlimb transfer of DA adaptation to the NDA, we compared the 10 NDA  
251 movements toward the central target (0 deg.) of the PRE-exposure phase to the first NDA  
252 movement of the POST-exposure phase (toward the central target). The transfer value of each  
253 participant was defined as the initial direction of the 1<sup>st</sup> trial made during the POST-exposure  
254 NDA phase minus the mean of the initial direction of 10 trials made toward the central target  
255 (0 deg.) during the PRE-exposure NDA phase. All data had a normal distribution as verified  
256 with the Kolmogorov-Smirnov method. Newman-Keuls tests were used for post-hoc analysis.  
257 For all tests, the significance threshold was set at 0.05.

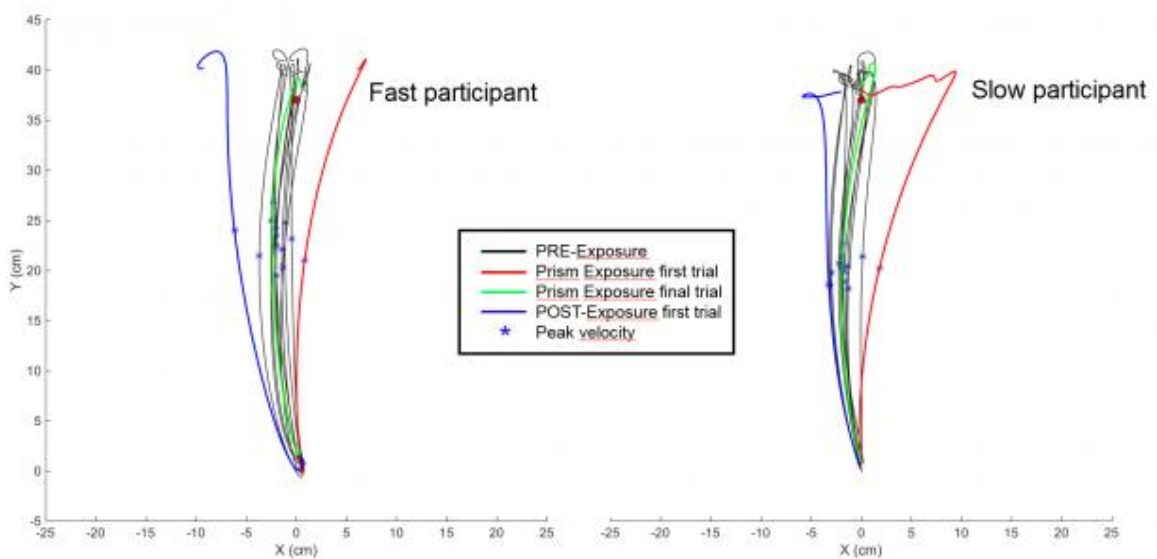
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259

260 **Results**

261 *Prismatic adaptation of dominant arm movements*

262 During the PRE-exposure experimental phase used to determine baseline performance,  
263 reaching movements were generally accurate (mean  $\pm$  SD final error= $0.3 \pm 0.5$  deg.) despite  
264 their high velocity (mean peak velocity across targets= $3.2 \pm 0.7$  m/s). Most kinematic  
265 parameters did not substantially vary across the three phases of the session (PRE-exposure,  
266 Prism exposure and POST-exposure) as ANOVAs showed no significant difference across  
267 experimental phases (mean peak velocity across targets, arms and conditions= $3.1 \pm 0.8$  m/s,  
268  $F(2,38)=0.1$ ,  $p=0.87$ ,  $\eta^2=0.007$ ; time to peak velocity= $154 \pm 31$  ms,  $F(2,38)=0.13$ ,  $p=0.88$ ,  
269  $\eta^2=0.005$ ; peak acceleration = $43.8 \pm 16.4$  m/s<sup>2</sup>,  $F(2,38)=1.8$ ,  $p=0.19$ ,  $\eta^2=0.08$ ; time to peak  
270 acceleration= $86 \pm 32$  ms,  $F(2,38)=1.1$ ,  $p=0.33$ ,  $\eta^2=0.04$ ; movement time= $435 \pm 103$  ms;  
271  $F(2,38)=2.7$ ,  $p=0.08$ ,  $\eta^2=0.12$ ).

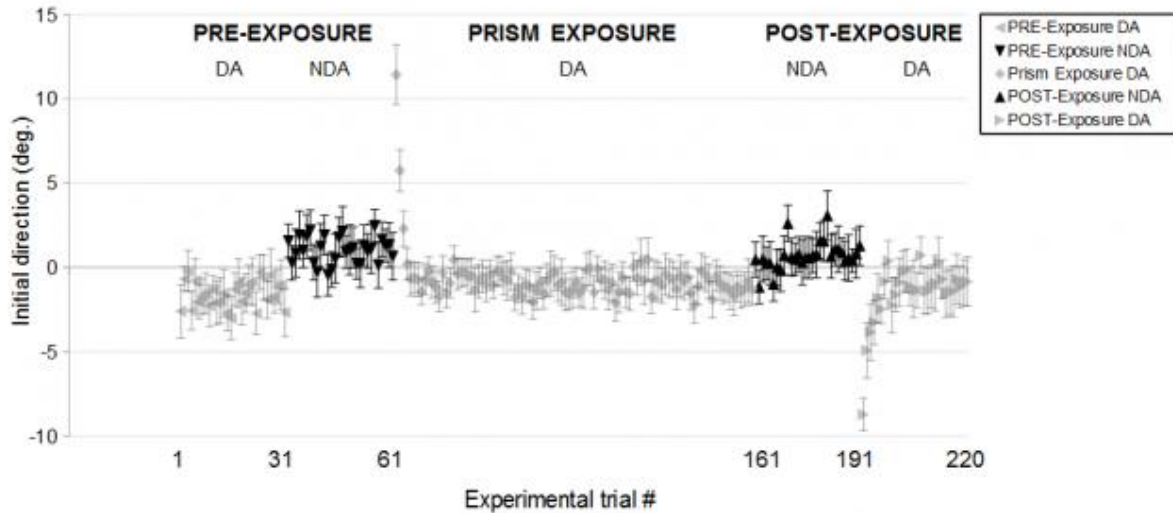


272  
273 *Figure 2: Prism adaptation, illustrated with a top view of reaching movements with the*  
274 *dominant arm for a fast participant (mean peak velocity across the experiment= $3.9$  m/s) and*  
275 *a slow participant (mean peak velocity across the experiment= $2.1$  m/s). (Color required for*  
276 *printed version).*

277  
278 When participants had to wear prisms, which deviated the visual field to the right (thus  
279 including the seen target which differed from its physical location), movement trajectory of

280 the first trial was deviated to the right. Compared to the fast participants, slower participants  
281 had more time to visually compare hand and target positions and to correct for movement  
282 errors. This can be seen in Figure 2 which illustrates the motor behavior of two participants  
283 with different movement speeds. While all participants saw their hand going rightward with  
284 respect to the target, slower participants could adjust the arm trajectory during the course of  
285 the movement.

286         Adaptation was revealed by the reduction, trial after trial, of final errors as well as  
287 trajectory errors, which eventually became similar to baseline (Figure 3, grey dots). Only the  
288 central target was used during the Prism exposure phase and when only considering  
289 movements toward the central target throughout the experiment, a one-way ANOVA [PHASE  
290 (PRE-exposure, Prism exposure 1<sup>st</sup> trial, 2<sup>nd</sup> trial, 3<sup>rd</sup> trial, 4<sup>th</sup> trial and 100<sup>th</sup> trial, POST-  
291 exposure 1<sup>st</sup> trial)] showed a significant effect of the experimental PHASE on initial  
292 movement direction ( $F(6,114)=55.9$ ,  $p=0.0000$ ,  $\eta^2=0.75$ ). Post-hoc comparisons revealed  
293 that, as shown in Figure 4A, initial direction was significantly deviated to the right for the first  
294 trial of the Prism exposure phase compared to baseline, i.e. to the mean of the 10 movements  
295 toward the central target in the PRE-exposure phase; the shift was +12.8 deg. on average  
296 across participants. Initial direction of the second and third movements of the Prism exposure  
297 phase also differed from baseline, but the initial direction of the fourth trial did not  
298 significantly differ from baseline, suggesting that it took about four trials for participants to  
299 adapt to the prism perturbation; the average number of trials for movements to fall back  
300 within the 95% confidence interval of the baseline was  $4.7 \pm 2.6$  trials.



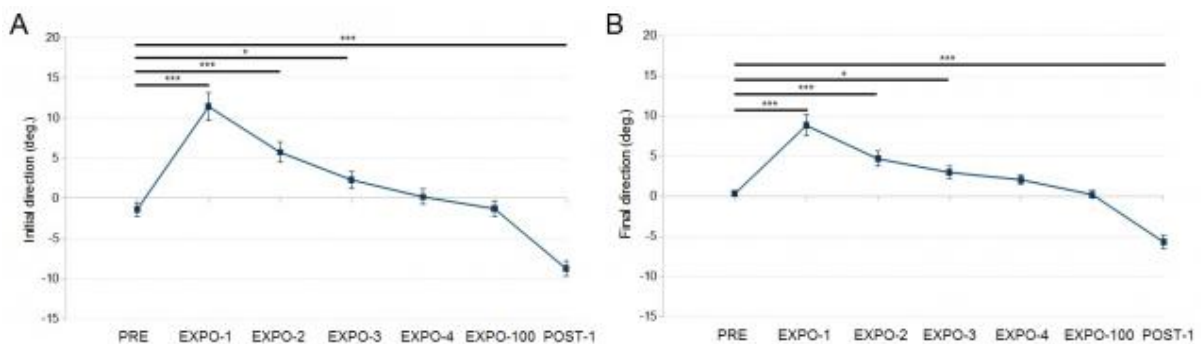
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302 *Figure 3: Prism adaptation, illustrated with initial direction averaged across participants as*  
 303 *a function of the experimental conditions. Error bars represent standard errors.*

304

305 Prisms also influenced final reach accuracy (Figure 4B). This was statistically  
 306 significant as an ANOVA [PHASE (PRE-exposure, Prism exposure 1<sup>st</sup> trial, 2<sup>nd</sup> trial, 3<sup>rd</sup> trial,  
 307 4<sup>th</sup> trial and 100<sup>th</sup> trial, POST-exposure 1<sup>st</sup> trial)] showed an effect of the experimental  
 308 PHASE on final direction ( $F(6,114)=42.1$ ,  $p=0.0000$ ,  $\eta^2=0.69$ ). Final direction was deviated  
 309 rightward on the first trial of the Prism exposure phase compared to baseline (the shift was  
 310 +8.5 deg. on average across participants). This analysis also suggests that adaptation occurred  
 311 in about 4 trials.

312



313

314 *Figure 4: Prism adaptation, illustrated with initial direction (A) and final direction (B) across*  
 315 *experimental trials with the dominant arm. Data points represent the mean of 10 trials toward*  
 316 *the central target during PRE-exposure, the 1<sup>st</sup>, 2<sup>nd</sup>, 3<sup>rd</sup>, 4<sup>th</sup> and 100<sup>th</sup> trial of the Prism*

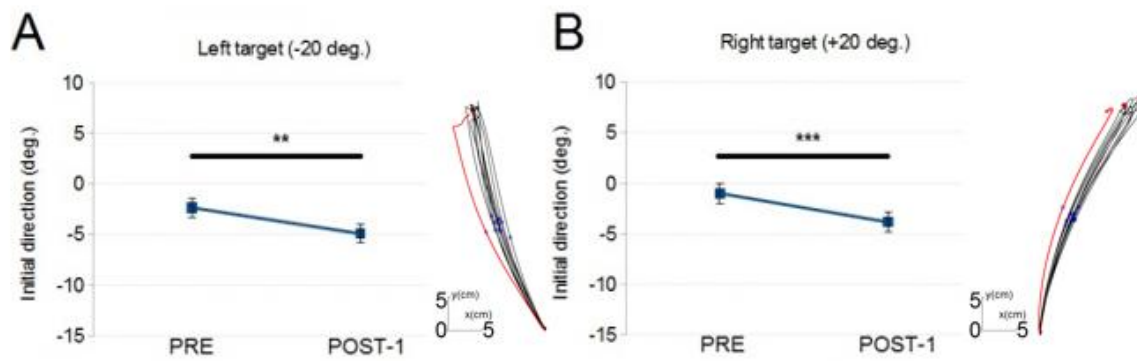
317 *exposure phase, and the 1<sup>st</sup> trial of the POST-Exposure phase. Error bars represent standard*  
318 *errors. \* $p < 0.05$  \*\*\* $p < 0.001$ , significant difference. (Color not required for printed version).*

319

320         After the Prism exposure phase, the rightward-deviating prisms were removed. Figures  
321 2, 3 and 4 show that following the POST-exposure phase testing the non-dominant arm,  
322 leftward after-effects were still observed on the dominant arm. Indeed, the first trial during the  
323 POST-exposure phase with the dominant arm was deviated to the left compared to the PRE-  
324 exposure phase (mean leftward shift in initial direction=7.3 deg.; mean shift in final  
325 direction=6.0 deg.). The after-effect was systematic: when assessed for each participant by  
326 comparing initial direction in the first trial of POST-exposure to the 95% confidence interval  
327 of the baseline trials, the after-effect was significant for every single participant, further  
328 reflecting prism adaptation.

329         While reaching movements were made only toward the central target during the Prism  
330 exposure phase, different target directions were tested during the PRE- and the POST-  
331 exposure phase to determine whether prism adaptation generalized across movement  
332 directions. Figure 5 shows that after-effects were also found for the lateral targets. A t-test  
333 showed a significant difference between initial direction of the first DA movement toward the  
334 left target during the POST-exposure phase and the mean of the 10 trials made toward the left  
335 target during the DA PRE-exposure phase ( $t(20)=3.07$ ;  $p=0.006$ ; Cohen's  $d=0.04$ ; see Figure  
336 5A). An equivalent difference was seen for DA reaches to the right target ( $t(20)=4.18$ ;  
337  $p=0.0005$ ; Cohen's  $d=0.04$ ; see Figure 5B). These findings indicate generalization of prism  
338 adaptation across target directions. Such generalization was also statistically significant when  
339 analyzing final direction (for the left target:  $t(20)=7.04$ ;  $p=0.0000$ ; Cohen's  $d=0.15$ ; and for  
340 the right target:  $t(20)=3.74$ ;  $p=0.001$ ; Cohen's  $d=0.1$ ).





341

342 *Figure 5: Generalization of prism adaptation across movement directions, illustrated with*  
 343 *initial direction of the dominant arm (DA) toward the left target (A) and right target (B) for*  
 344 *the PRE-exposure phase (mean of 10 trials) and the 1<sup>st</sup> trials of the POST-exposure phase*  
 345 *toward the corresponding target. Error bars represent standard errors. \*\* $p < 0.01$*   
 346 *\*\*\* $p < 0.001$ , significant difference. Insets present top views of dominant arm movements*  
 347 *during the PRE-exposure phase (black lines) and the first trial of the POST-exposure phase*  
 348 *(red line). (Color required for printed version).*

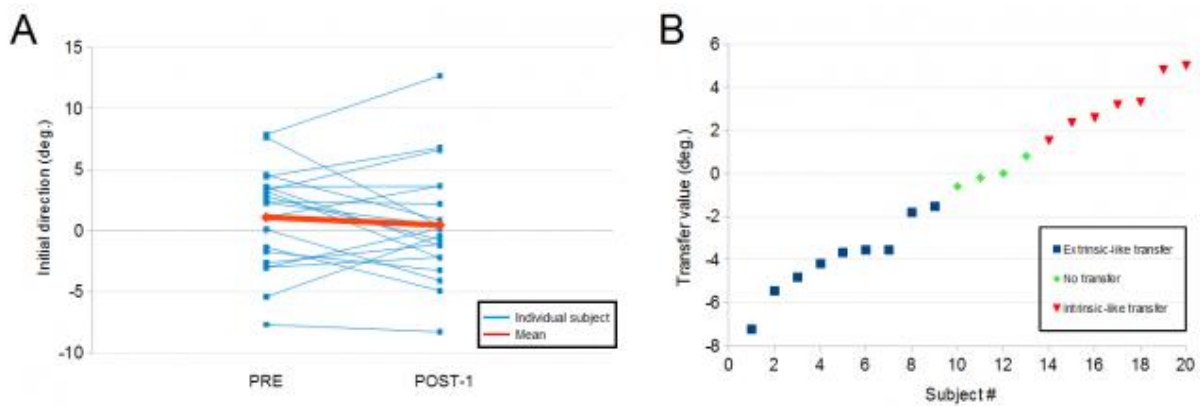
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### 351 *Heterogeneity of interlimb transfer of prism adaptation*

352 While prism adaptation and its generalization across directions were significant for the  
 353 dominant arm across the group of 20 participants, there was no evidence of interlimb transfer  
 354 at the group level (Figure 3, black dots, and 6). A t-test showed no significant difference  
 355 between initial direction of the first movement (toward the central target) during NDA POST-  
 356 exposure phase and the mean initial direction of the 10 trials made toward the same target  
 357 during the NDA PRE-exposure phase ( $t(20)=0.8$ ;  $p=0.43$ ). In line with this finding, t-tests  
 358 revealed no significant differences in initial direction when comparing the first NDA  
 359 movement of the POST-exposure toward one of the lateral targets to the corresponding PRE-  
 360 exposure (Left target:  $t(19)=0.5$ ;  $p=0.63$ ; Right target:  $t(20)=1.0$ ;  $p=0.32$ ). The analysis of  
 361 final direction resulted in similar findings, i.e., the first NDA movement toward each target  
 362 did not differ from its respective baseline (Central target:  $t(20)=0.43$ ,  $p=0.68$ ; Left target:  
 363  $t(19)=0.45$ ,  $p=0.66$ ; Right target:  $t(20)=0.28$ ,  $p=0.79$ ).

364

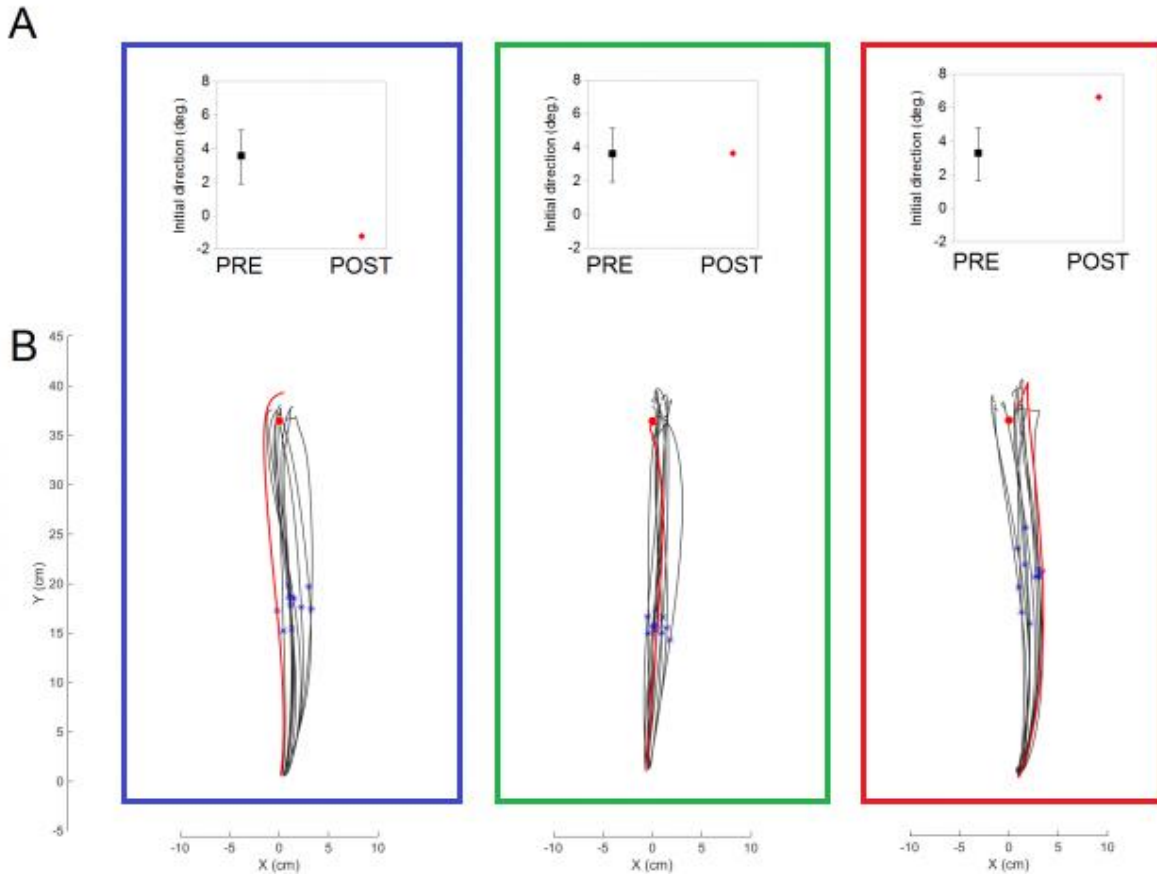


365

366 *Figure 6: A/ Initial direction of each participant with the non-dominant arm (blue lines)*  
367 *across the PRE-exposure phase (mean of 10 trials) and for the 1<sup>st</sup> trial of the POST-exposure*  
368 *phase. The mean initial direction across all participants is in red line. B/ Transfer value*  
369 *(POST-1 – PRE) of each participant. (Color not required for printed version).*

370

371 Interlimb transfer was not significant because of large inter-individual differences, as shown  
372 in Figures 6A and 6B. To determine whether interlimb transfer was present or not for each  
373 participant, we computed a 95% confidence interval from all movements made by each  
374 individual during the PRE-exposure of the NDA toward the central target. When the initial  
375 direction of the first trial of POST-exposure NDA phase was within the confidence interval,  
376 transfer was not considered to be significant. When the initial direction of the first trial of  
377 POST-exposure NDA phase was below the lower limit of this confidence interval, transfer  
378 was considered as leftward (opposite to the rightward prism shift) and referred to as  
379 ‘extrinsic-like’ (Figure 7). In contrast, if it was greater than the upper limit of the confidence  
380 interval, transfer was rightward and referred to as ‘intrinsic-like’. This analysis revealed that 9  
381 participants exhibited transfer in the leftward (extrinsic-like) direction, 7 participants  
382 exhibited rightward (intrinsic-like) transfer and 4 participants exhibited no transfer: such  
383 heterogeneity clearly appears on Figure 6B and Figure 7, which highlights the continuum of  
384 interlimb transfer across participants.



385

386 *Figure 7: Examples of interlimb transfer for three participants. A/ 95% Confidence intervals*  
 387 *built from PRE-exposure data (black), contrasted with the first trial of the POST-exposure*  
 388 *phase (red). B/ Top views of reaching movements with the non-dominant arm during the PRE-*  
 389 *exposure phase (black lines) and the first trial of the POST-exposure phase (red line). In the*  
 390 *left column, the first POST-exposure trial falls outside the confidence interval and the*  
 391 *interlimb transfer is consistent with an ‘extrinsic-like’ movement representation. In the*  
 392 *central column, there is no transfer and in the right column, transfer is ‘intrinsic-like’.*  
 393 *(Color required for printed version).*

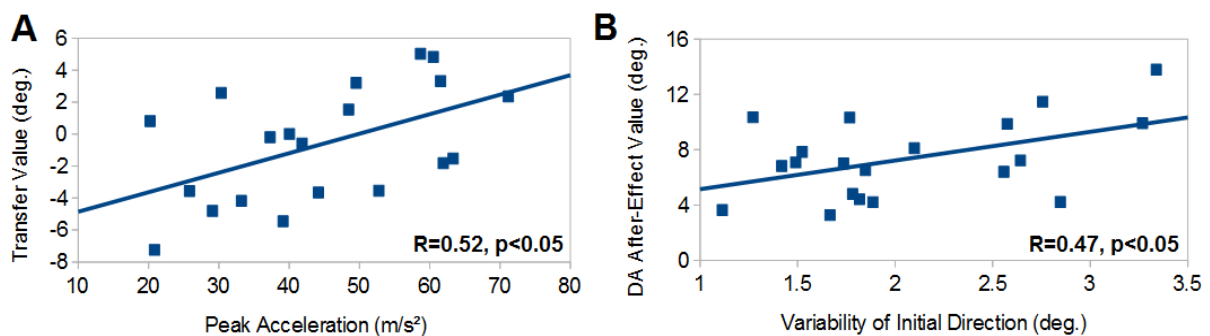
394

395 *Individual kinematic features correlate with the interlimb transfer value and after-effects of*  
 396 *sensorimotor adaptation*

397 We aimed to determine whether individual characteristics of participants could be linked to  
 398 the magnitude of transfer from the dominant to the non-dominant arm. We first assessed the  
 399 influence of handedness on sensorimotor adaptation, but no significant correlation was found  
 400 between handedness and transfer value ( $r=-0.22$ ;  $p=0.35$ ); handedness did not significantly  
 401 influence or correlate with any measure related to sensorimotor adaptation or transfer.  
 402 However, it has been suggested that movement variability and velocity could influence

403 sensorimotor adaptation (Kitazawa et al. 1997; Wu et al. 2014; Pekny et al. 2015; Lefumat et  
 404 al. 2015; Therrien et al. 2016) and also distinguished the early and late phases of adaptation in  
 405 terms of underlying mechanisms (Smith et al. 2006; Wolpert et al. 2011). We thus  
 406 investigated the influence of peak velocity, peak acceleration and variable trajectory errors  
 407 throughout adaptation or specifically during the early and late phases of Prism exposure (first  
 408 and last 10 exposure trials). We found that interlimb transfer was correlated with variables  
 409 typically associated to movement vigor, such as peak acceleration and peak velocity (Mazzoni  
 410 et al. 2007; Reppert et al. 2018). Figure 8A shows a positive linear correlation between the  
 411 transfer value and the mean peak acceleration averaged across the Prism exposure phase ( $PA$   
 412  $= 0.1 \times \text{transfer value} - 6$ ;  $r=0.52$ ;  $p=0.02$ ). Low peak acceleration reflected a negative  
 413 transfer value (Figure 8A) and therefore extrinsic transfer while high peak acceleration  
 414 reflected a positive transfer value and therefore intrinsic transfer. As expected across the  
 415 Prism exposure phase, peak acceleration was correlated with peak velocity ( $r=0.96$ ;  
 416  $p=0.0000$ ). Peak velocity was also positively correlated with the transfer value ( $r=0.48$ ;  
 417  $p=0.03$ ).

418

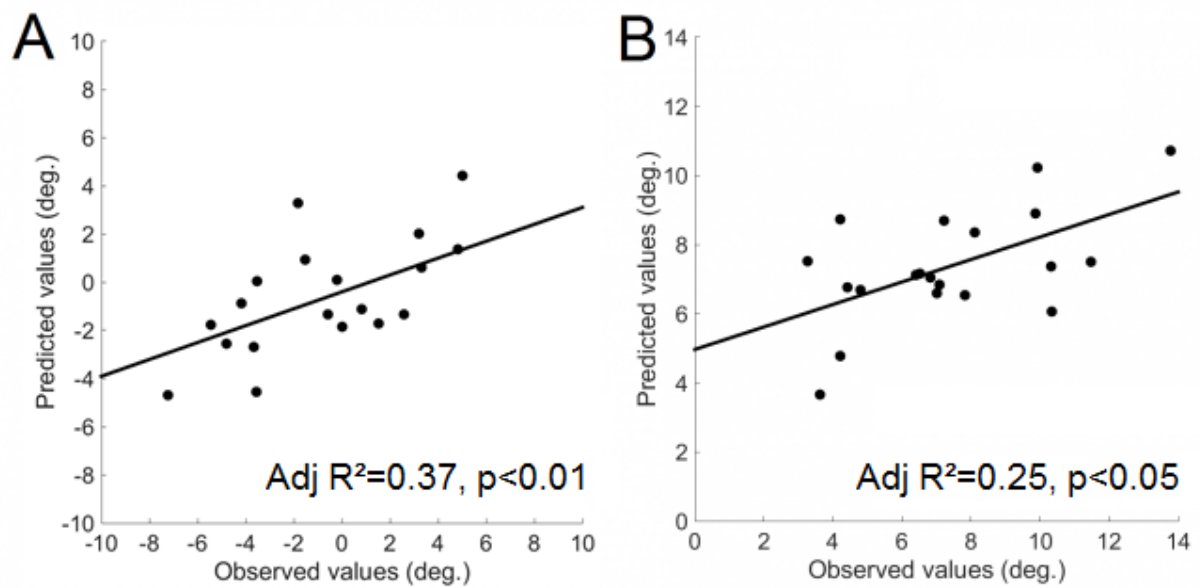


419

420 *Figure 8: A/ Correlation between interlimb transfer and mean peak acceleration averaged*  
 421 *across the prism exposure phase. B/ Correlation between DA after-effect and variability of*  
 422 *initial direction of the ten last trials of the prism exposure phase. (Color not required for*  
 423 *printed version).*

424

425 To examine whether the magnitude of interlimb transfer could be correlated to a  
426 combination of kinematic variables measured in early and late exposure phases, we used a  
427 multiple regression analysis. A forward-stepwise method (accepting the most powerful  
428 predictor first) revealed that variables such as, first, mean peak acceleration during the Prism  
429 exposure phase and, second, variability of initial direction at the end of the Prism exposure  
430 phase (last 10 trials) could be correlated with the observed transfer value [ $F(2,17)=6.6$ ;  
431  $r^2=0.44$ ; adjusted  $r^2=0.37$ ;  $p=0.007$ ]. The equation of the multiple regression was as follows:  
432 transfer value =  $-11.41 + 0.14 \times PA + 2.28 \times$  variability of initial direction, indicating that the  
433 greater the peak acceleration, the greater the variability, the greater the transfer value. Low  
434 peak acceleration and low variability reflected extrinsic transfer while high peak acceleration  
435 and high variability reflected intrinsic transfer. The contributions of peak acceleration  
436 ( $p=0.006$ ) and variability ( $p=0.036$ ) were both significant. Adding more kinematic variables  
437 increased the percentage of explained variance (which reached 93% with 9 variables for  
438 instance, including peak velocity and number of trials to adapt); we only report results with 2  
439 variables for the sake of clarity. Figure 9A shows the relationship between the observed and  
440 predicted transfer values based on the equation of the 2-variable multiple regression.



441

442 *Figure 9: A/ Observed versus predicted transfer based on a multiple regression with two*  
 443 *measures, peak acceleration across the Prism exposure phase and variability of initial*  
 444 *direction in the late exposure phase (last 10 trials). B/ Observed versus predicted DA after-*  
 445 *effect (absolute value), based on a multiple regression using variability of initial direction in*  
 446 *late exposure and number of exposure trials to adapt. (Color not required for printed*  
 447 *version).*

448

449 We investigated a potential link between the transfer value and the after-effect value  
 450 on the DA, but no significant correlation was found ( $r=-0.37$ ;  $p=0.1$ ). For the following  
 451 analyses, we used the absolute value of the after-effect for clarity purposes (because all  
 452 participants were deviated in the same direction during the DA POST-exposure 1<sup>st</sup> trial, so the  
 453 greater the after-effect value, the more deviated to the left is the participant compared to  
 454 his/her PRE-exposure phase). We found a positive linear correlation between variability of  
 455 initial direction during the late exposure phase (last 10 trials) and the after-effect (Figure 8B;  
 456  $r=0.47$ ;  $p=0.04$ ). We also examined whether the magnitude of after-effect found on the DA  
 457 could be correlated with kinematic data by using a multiple regression analysis, as we did for  
 458 interlimb transfer. A forward-stepwise multiple regression revealed that late-exposure  
 459 variability and the number of trials to adapt were the first two variables correlated with the  
 460 observed after-effect value [ $F(2,17)=4.1$ ;  $r^2=0.32$ ; adjusted  $r^2=0.25$ ;  $p=0.03$ ]. The multiple

461 regression equation was: absolute after-effect value =  $-5.03 + 1.91 \times \text{variability} - 0.35 \times$   
462 number of trials, indicating that the greater the variability and the fewer trials needed to adapt,  
463 the greater the after-effect. Figure 9B shows the relationship between the observed and the  
464 predicted after-effect values based on the equation of the multiple regression.

465

466 *Interlimb transfer is not significantly influenced by the awareness of motor errors*

467 Only one participant answered that he was not consciously aware of the errors made during  
468 the beginning of the exposure phase, although his initial direction was shifted by 6.5 deg.  
469 compared to his baseline. When asked whether they associated their errors to external factors,  
470 participants tended to agree (mean score= $8.0 \pm 2.3$  with 10 indicating 'strongly agree'). When  
471 asked whether they associated the errors they made in the exposure phase to themselves,  
472 participants tended to disagree (mean score= $2.7 \pm 3.0$ ). When participants had to report  
473 whether they assigned trajectory errors to 'internal factors' (0) or 'external factors' (10), they  
474 tended to assign their errors to external factors (mean score= $7.8 \pm 2.2$ ). No significant  
475 correlation was found between the transfer value and the assignment of errors (all  $r < 0.08$ ; all  
476  $p > 0.51$ ).

477 With respect to the question 'internal factors' or 'external factors', only 3 of the  
478 participants pointed toward 'internal factors' (mean score= $4.1 \pm 0.8$ ). When these 3  
479 participants were asked 'Did you associate the errors you made in the exposure phase to  
480 yourself?', all of them agreed (mean score= $7.0 \pm 1.4$ ). These 3 participants did not agree  
481 when asked 'Did you associate the errors you made early in the Exposure phase to external  
482 factors?' (mean score= $3.4 \pm 0.3$ ). The 17 other participants assigned their trajectory errors to  
483 external factors (mean score= $8.4 \pm 1.6$ ). A Mann-Whitney non-parametric test showed that  
484 the transfer value did not significantly depend on the assignment of errors (mean of 3

485 participants reporting ‘internal factors’  $= -1.0 \pm 5.1$  deg.; mean of 17 participants reporting  
486 ‘external factors’  $= -0.6 \pm 3.5$  deg.;  $p=0.71$ ).

487

488

## 489 **Discussion**

490 We aimed to test the hypothesis that specific features of movements can influence the  
491 interlimb transfer of sensorimotor adaptation. We used a well-known visuomotor perturbation  
492 (prismatic glasses) to induce sensorimotor adaptation and assessed generalization across  
493 directions and interlimb transfer (Harris 1963; Martin et al. 1996; Kitazawa et al. 1997;  
494 Morton & Bastian 2004; Michel et al. 2007). Prisms have been used to study the process of  
495 visuomotor adaptation since the pioneering work of von Helmholtz (1867) and Stratton  
496 (1896) and the acquired knowledge has been valuable, for instance for the rehabilitation of  
497 strabismus or spatial neglect (Rossetti et al. 1998). For the practical purpose of personalized  
498 training (Seidler et al. 2015) as well as for a better understanding of the factors which  
499 influence transfer of sensorimotor adaptation, we re-investigated the interlimb transfer of  
500 prism adaptation with detailed analyses of movement kinematics for each individual.

501

### 502 *Generalization of prismatic adaptation across movement directions*

503 A classical pattern of prism adaptation was observed with the dominant arm: as in previous  
504 studies (Redding & Wallace 1988; Martin et al. 1996; Sarlegna et al. 2007; O’Shea et al.  
505 2014), initial errors due to the prisms were reduced trial-by-trial and when prisms were  
506 removed, clear after-effects were observed with the trained limb. Such after-effects were  
507 observed after participants reached to the same central target as in the Prism exposure phase.  
508 After-effects were also observed on the two other lateral targets, consistent with previous  
509 reports of generalization of sensorimotor adaptation across movement directions for prism



510 adaptation (Redding & Wallace 2006), visuomotor rotations (Ghahramani et al. 1996;  
511 Krakauer et al. 2000) and adaptation to force fields (Thoroughman & Shadmehr 2000; Malfait  
512 et al. 2002; Lefumat et al. 2015).

513         A prismatic perturbation biases all visual inputs, including vision of the environment,  
514 the target and the arm, and would seem to facilitate generalization across the workspace or  
515 even across tasks or limbs. For instance, generalization of prism adaptation has been  
516 previously reported across upper-limb segments in a proximodistal direction (Hay and  
517 Brouchon 1972; see also Krakauer et al. 2006) and from a walking task to a reaching task  
518 (Morton and Bastian 2004). Generalization seems to be often found between tasks involving  
519 similar joints (Alexander et al. 2011) or when adaptation involves higher-order, cognitive  
520 processes (Morton & Bastian 2004; Malfait & Ostry 2004; McDougle et al. 2016).

521

#### 522 *Interlimb transfer of prismatic adaptation*

523 To determine whether sensorimotor adaptation is limb specific, a classic test is to determine  
524 whether adaptation with one arm influences the opposite arm. As early as 1963, Harris  
525 reported that interlimb transfer of prism adaptation was limited. In the present study,  
526 interlimb transfer was not significant at the group level and a large heterogeneity across  
527 participants was uncovered. This appears to be consistent with the heterogeneity of findings  
528 in the literature. At an individual level, we found that for some of the participants (N=4),  
529 there was no interlimb transfer of prism adaptation, in line with the overall finding in several  
530 previous studies (Kitazawa et al. 1997; Martin et al. 1996; Michel et al. 2007). For other  
531 participants (N=9), interlimb transfer was observed in the form of leftward after-effects on  
532 the non-dominant arm, which could reflect the leftward compensation of the rightward  
533 prism deviation, in extrinsic or visual space (Harris 1963; Cohen 1967; Cohen 1973; Taub &  
534 Goldberg 1973; Choe & Welch 1974; Wallace & Redding 1979). However, a second,

535 intrinsic coordinate system can be considered (Criscimagna-Hemminger et al. 2003; Galea  
536 et al. 2007; Wiestler et al. 2014; Franklin et al. 2016). Representation in this coordinate  
537 system predicts mirror-symmetric interlimb transfer with respect to the sagittal plane. In our  
538 study, rightward interlimb transfer was observed in one third of the group (N=7), which may  
539 reflect the encoding of sensorimotor adaptation in intrinsic space. This finding was  
540 unexpected but is consistent with the work of Kalil and Freedman (1966) which reported a  
541 large heterogeneity in interlimb transfer of prism adaptation. In particular, they reported that  
542 two out of nine participants exhibited transfer which was consistent with an encoding of  
543 prism adaptation in intrinsic coordinates.

544         One can speculate that behavioral heterogeneity, such as observed in the present  
545 study, is related to the heterogeneity of the brain structures (Gazzaniga et al. 1998; ten  
546 Donkelaar et al. 2004; Sun et al. 2016) or of the idiosyncratic representations underlying  
547 visuomotor and force-field adaptation, as they appear to be encoded in both extrinsic and  
548 intrinsic coordinates (Brayanov et al. 2012; Carroll et al. 2014; Wiestler et al. 2014;  
549 Berniker et al. 2014; Parmar et al. 2015). The presence in pre-motor and motor areas of both  
550 extrinsic-like and intrinsic-like representations (Takei et al. 1999; Takei et al. 2001;  
551 Wiestler et al. 2014) may explain why interlimb transfer can be so heterogeneous across  
552 studies, even when similar perturbations are used. Indeed, conflicting findings have been  
553 reported for prism adaptation but also for adaptation to new limb dynamics (Criscimagna-  
554 Hemminger et al. 2003; Malfait & Ostry 2004; Galea et al. 2007; Stockinger et al. 2015;  
555 Lefumat et al. 2015). Next, we address the issue of whether one can make sense of that  
556 heterogeneity.

557

558 *On the correlation between kinematic variables, interlimb transfer and after-effects*

559 Heterogeneity between individuals is inevitable when considering the idiosyncratic properties  
560 of the central nervous system for any given individual (Gazzaniga et al. 1998; Kanai & Rees  
561 2011). In the present study, a continuum of transfer values was observed. Regression analyses  
562 showed that kinematic variables selected during the Prism exposure phase can be correlated  
563 with the transfer value of each participant. We found that peak acceleration and peak velocity  
564 during prism exposure, as well as variability of initial direction at the end of the exposure  
565 phase, were related to interlimb transfer. Mazzoni et al. (2007) as well as Reppert et al. (2018)  
566 highlighted how variables related to movement vigor, peak velocity or peak acceleration, for  
567 instance, vary across individuals, possibly because of differences in perceived motor cost.  
568 Kitazawa et al. (1997) previously highlighted the importance of peak velocity in prism  
569 adaptation when they showed that the magnitude of the after-effect depends on the velocity  
570 difference between movements during and after the exposure phase (see also Mattar & Ostry  
571 2010).

572 In the present study, a higher peak acceleration (and peak velocity) was found for  
573 participants who transferred in an intrinsic coordinate system, while a lower peak acceleration  
574 corresponded to an extrinsic coordinate system. The influence of movement kinematics on  
575 interlimb transfer may be mediated by the attribution of motor errors to different sources,  
576 which has been suggested to be key for the pattern of generalization of sensorimotor  
577 adaptation (Berniker & Kording 2008). However, assessing error-attribution is difficult and  
578 our questionnaire-based approach failed to reveal a significant link between the source of  
579 motor errors and interlimb transfer.

580 A parsimonious interpretation of these findings is that the way the new sensorimotor  
581 mapping was learned during exposure influenced subsequent movements, including those  
582 used to assess interlimb transfer. This is consistent with the idea that generalization of  
583 sensorimotor adaptation depends on the history of prior actions (Krakauer et al. 2006; Wei &

584 Kording 2009). An alternative hypothesis is that there is a possible link between the  
585 speed/acceleration of a movement and the nature of its neural representation. This may be  
586 related to the idea that faster movements mostly rely on feedforward control, because less  
587 time is available to process peripheral sensory feedback during movement execution.  
588 Feedforward motor control describes how motor neurons control muscles without using  
589 sensory feedback, most likely with signals in an intrinsic, muscle-based coordinate system  
590 (Tanaka & Sejnowski 2013). Slower movements can be controlled with online feedback to  
591 adjust the hand path, and the importance of visual feedback in human movement control has  
592 been highlighted (Reichenbach et al. 2014; Sarlegna & Mutha 2015). The fact that visual  
593 feedback control relies on the use of signals originally in extrinsic, retina-based coordinates,  
594 may be related to the encoding of slower visually-guided movements in extrinsic coordinates.  
595 Hence our findings suggest that movement vigor could explain the heterogeneity of interlimb  
596 transfer reported in previous prism adaptation studies, in which unfortunately movement  
597 speed or acceleration was rarely reported.

598         Our findings showed that variability of initial direction during the Prism exposure  
599 phase was positively correlated with interlimb transfer to the non-dominant arm and to after-  
600 effects on the adapted limb. High motor variability reflected intrinsic transfer while low  
601 variability reflected extrinsic transfer. Variability is often considered to reflect noise in the  
602 nervous system (Faisal et al. 2008) but recent findings highlighted how it can also reflect  
603 exploration strategies and may benefit sensorimotor adaptation (Wu et al. 2014; Herzfeld &  
604 Shadmehr 2014; Lefumat et al. 2015; Therrien et al. 2016; Lefumat et al. 2016; but see He et  
605 al. 2016). For instance, Lefumat et al. (2015) found that participants who were more variable  
606 when adapting to novel limb dynamics showed greater interlimb transfer. Our results on a  
607 different type of adaptation (Haith & Vijayakumar 2009; Sarlegna & Bernier 2010; Donchin  
608 et al. 2012) support and extend the idea that variability of the motor output could influence

609 after-effects on the trained as well as the untrained arm. However, further work is necessary  
610 to understand the underlying mechanisms.

611         Handedness has been shown to affect interlimb transfer (Chase & Seidler 2008;  
612 Lefumat et al. 2015) so we recruited both right- and left-handers to provide a general model  
613 of interlimb transfer of prism adaptation. Lefumat et al. (2015) studied a population of 20  
614 strongly right-handed individuals and reported that laterality quotient influenced interlimb  
615 transfer of force-field adaptation. In our study, handedness or laterality quotient did not  
616 significantly influence interlimb transfer of prism adaptation. However, across right- and  
617 left-handers, a small set of movement characteristics such as movement acceleration or  
618 variability during exposure was correlated to interlimb transfer. Now that a few movement  
619 characteristics have been identified as related to interlimb transfer, further studies need to be  
620 conducted in order to explore a possible causal link between these features and interlimb  
621 transfer, for instance by assessing the effect of manipulating movement speed or variability.  
622 Alternatively, future work could determine whether a third factor is the key leading to the  
623 differences in, and the correlation between, kinematic variables and interlimb transfer.  
624 Finally, it should be noted that in the present study, after-effects were systematically found  
625 on the dominant arm in the POST-exposure phase that followed thirty non-dominant arm  
626 movements with true visual feedback. Thus, the de-adaptation of non-dominant arm  
627 movements did not completely wash out adaptation of the dominant arm. This indicates that  
628 if there is any interlimb transfer from the non-dominant to the dominant arm, it is not  
629 complete.

630

631         In conclusion, interlimb transfer resulted for some participants in a directional shift of  
632 non-dominant arm movements that was consistent with an encoding of visuomotor adaptation  
633 in extrinsic coordinates while, for other participants, interlimb transfer was consistent with an

634 encoding of sensorimotor adaptation in intrinsic coordinates. A detailed kinematic analysis  
635 was instrumental to find that individual movement features such as movement acceleration  
636 and variability were related to qualitative as well as quantitative aspects of sensorimotor  
637 adaptation and its transfer across limbs. Low peak acceleration and low variability displayed  
638 during the exposure phase were linked to an extrinsic type of transfer while high peak  
639 acceleration and high variability were linked to an intrinsic type of transfer. Overall, these  
640 findings on unconstrained movements support the idea that individual movement features  
641 could be linked to the way the nervous system learn new motor skills and generalize learning.  
642 The study also suggests that the preferred movement characteristics may be related to the  
643 preferred coordinate frames of action representations.

644

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649

650 **Conflict of interest:** All authors declare no conflict of interest.

651

652 **Compliance with Ethical Standards / Ethical approval:** All procedures performed in this  
653 study involving human participants were in accordance with the ethical standards of the  
654 institutional review board of the Institute of Movement Sciences and with the 1964 Helsinki  
655 declaration and its later amendments or comparable ethical standards.

656

657 **Informed consent:** Informed consent was obtained from all individual participants included  
658 in the study.

659 **Author contributions:** A.G.R., H.L., J.-L.V., L.B. and F.R.S. designed the experiment;  
660 A.G.R., H.L. and F.R.S. performed experiments; A.G.R. and F.R.S. analyzed data; A.G.R.  
661 prepared figures; A.G.R., H.L., J.-L.V., R.C.M., L.B., C.B. and F.R.S. interpreted results of  
662 experiments; A.G.R. and F.R.S. drafted manuscript; A.G.R., H.L., J.-L.V., R.C.M., L.B., C.B.  
663 and F.R.S. edited manuscript and approved the final version for submission.

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