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Renault, Alix G; Lefumat, Hannah; Miall, R Chris; Bringoux, Lionel; Bourdin, Christophe; Vercher, Jean-Louis; Sarlegna, Fabrice R

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4   Alix G. Renault[1] ✉, Hannah Lefumat[1,2], R. Chris Miall[3], Lionel Bringoux[1],

5   Christophe Bourdin[1], Jean-Louis Vercher[1] & Fabrice R. Sarlegna[1] ✉

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7   [1] Aix Marseille Univ, CNRS, ISM, Marseille, France

8   [2] Department of Neuroscience, University of Pennsylvania, Philadelphia, USA

9   [3] School of Psychology, University of Birmingham, Birmingham, UK

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11   Correspondence should be addressed to Alix Renault or Fabrice Sarlegna, Institute of

12   Movement Sciences, CNRS & Aix-Marseille University (UMR 7287), 163 av. de Luminy –

13   CP 910, 13009 Marseille. E-mail: alix.renault@univ-amu.fr or fabrice.sarlegna@univ-amu.fr

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22   **Running title:** Movement features, after-effects and interlimb transfer of adaptation

23

24

Abstract

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

Introduction

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

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

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 1st 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 1st 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.

258

259

Results

Prismatic adaptation of dominant arm movements

During the PRE-exposure experimental phase used to determine baseline performance, reaching movements were generally accurate (mean ± SD final error=0.3 ± 0.5 deg.) despite their high velocity (mean peak velocity across targets=3.2 ± 0.7 m/s). Most kinematic parameters did not substantially vary across the three phases of the session (PRE-exposure, Prism exposure and POST-exposure) as ANOVAs showed no significant difference across experimental phases (mean peak velocity across targets, arms and conditions=3.1 ± 0.8 m/s, $F_{(2,38)}$=0.1, p=0.87, η2=0.007; time to peak velocity=154 ± 31 ms, $F_{(2,38)}$=0.13, p=0.88, η2=0.005; peak acceleration =43.8 ± 16.4 m/s², $F_{(2,38)}$=1.8, p=0.19, η2=0.08; time to peak acceleration=86 ± 32 ms, $F_{(2,38)}$=1.1, p=0.33, η2=0.04; movement time=435 ± 103 ms; $F_{(2,38)}$=2.7, p=0.08, η2=0.12).
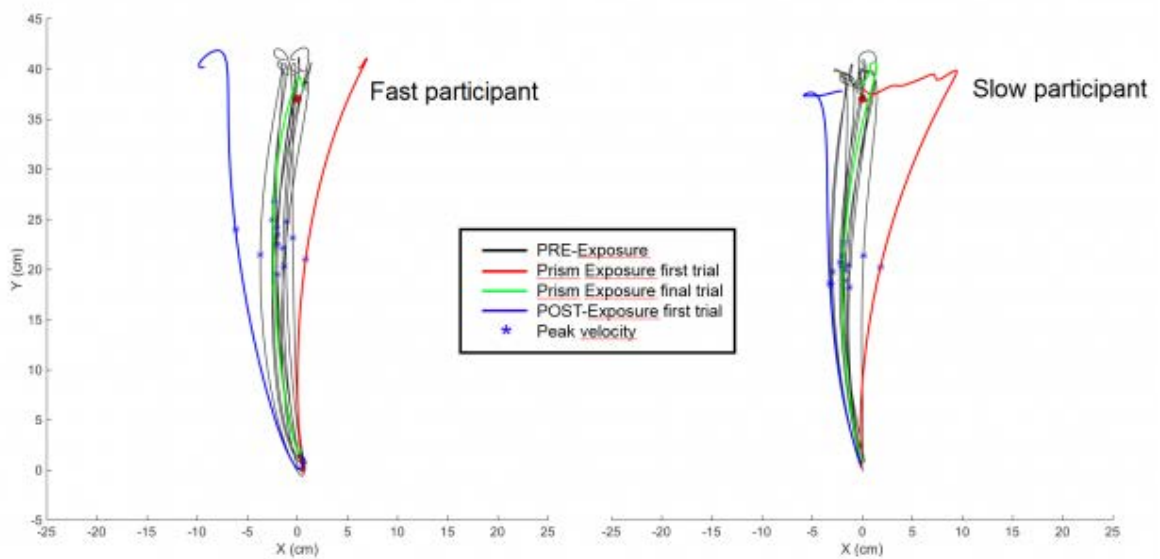
Figure 2: Prism adaptation, illustrated with a top view of reaching movements with the dominant arm for a fast participant (mean peak velocity across the experiment=3.9 m/s) and a slow participant (mean peak velocity across the experiment=2.1 m/s). (Color required for printed version).

When participants had to wear prisms, which deviated the visual field to the right (thus 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 1st trial, 2nd trial, 3rd trial, 4th trial and 100th trial, POST-

291 exposure 1st trial)] showed a significant effect of the experimental PHASE on initial

292 movement direction ($F_{(6,114)}=55.9$, $p=0.0000$, $\eta2=0.75$). 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 ± 2.6 trials.
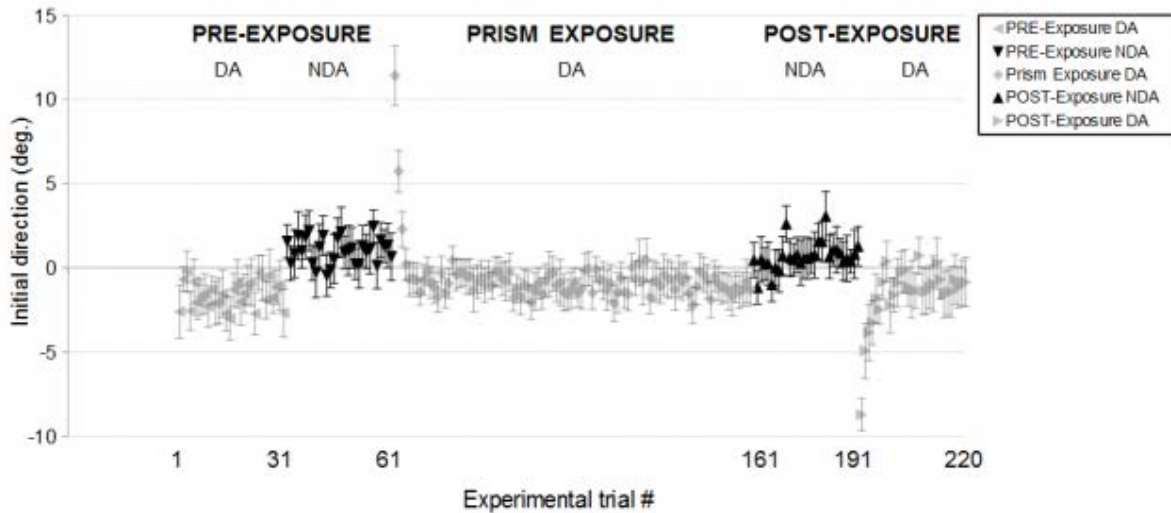
301

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 1st trial, 2nd trial, 3rd trial,

307 4th trial and 100th trial, POST-exposure 1st trial)] showed an effect of the experimental

308 PHASE on final direction ($F(6,114)=42.1$, $p=0.0000$, $\eta2=0.69$). 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
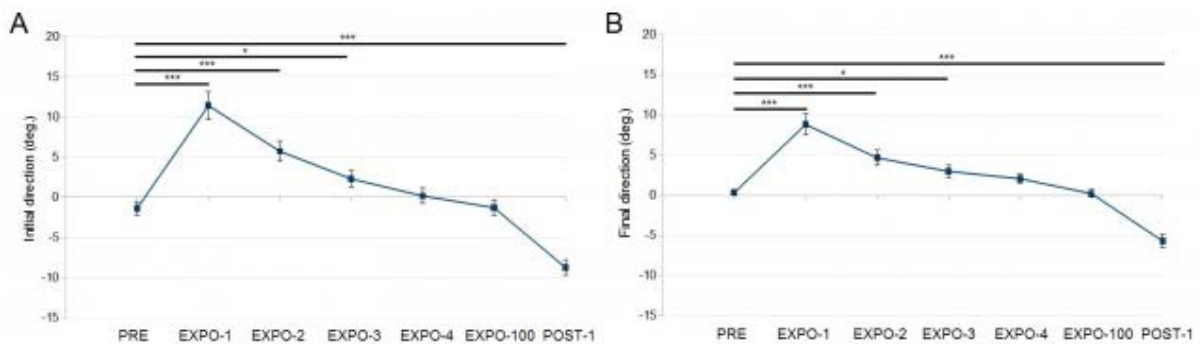
313

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 1st, 2nd, 3rd, 4th and 100th trial of the Prism*

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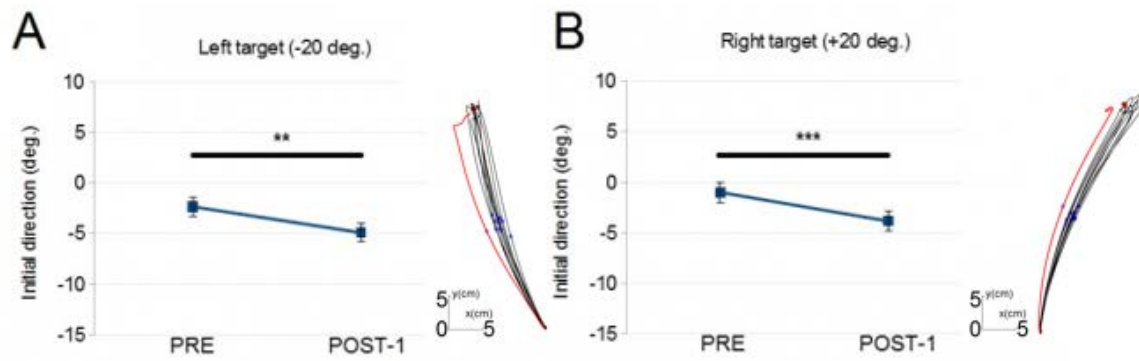
Figure 5: Generalization of prism adaptation across movement directions, illustrated with initial direction of the dominant arm (DA) toward the left target (A) and right target (B) for the PRE-exposure phase (mean of 10 trials) and the 1st trials of the POST-exposure phase toward the corresponding target.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

Heterogeneity of interlimb transfer of prism adaptation

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

364
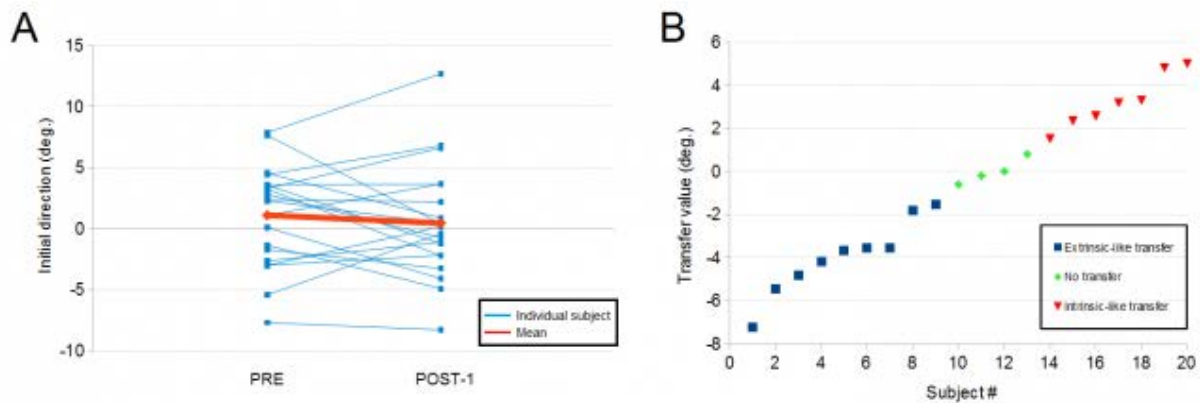
Figure 6: A/ Initial direction of each participant with the non-dominant arm (blue lines) across the PRE-exposure phase (mean of 10 trials) and for the 1st trial of the POST-exposure phase. The mean initial direction across all participants is in red line. B/ Transfer value (POST-1 – PRE) of each participant. (Color not required for printed version).

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

17
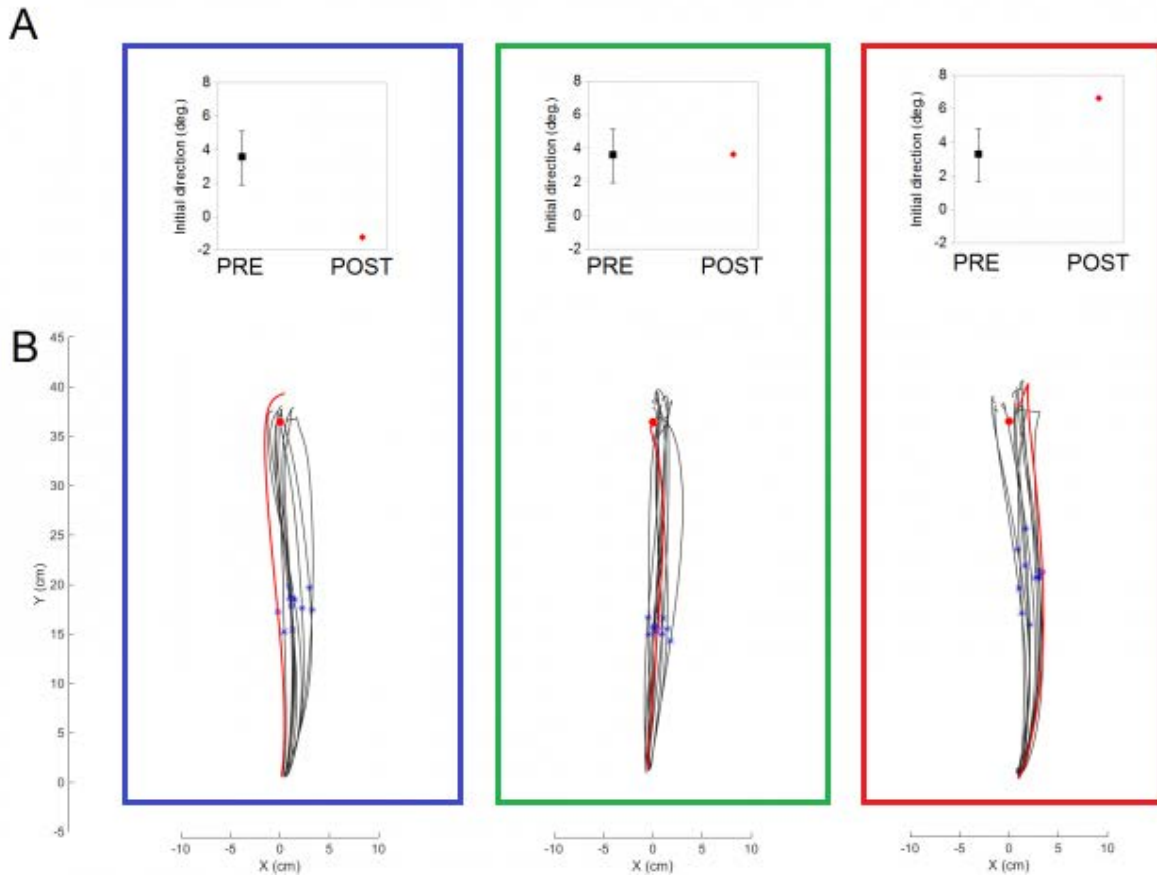
Figure 7: Examples of interlimb transfer for three participants. A/ 95% Confidence intervals built from PRE-exposure data (black), contrasted with the first trial of the POST-exposure phase (red). B/ Top views of reaching movements with the non-dominant arm during the PRE-exposure phase (black lines) and the first trial of the POST-exposure phase (red line). In the left column, the first POST-exposure trial falls outside the confidence interval and the interlimb transfer is consistent with an 'extrinsic-like' movement representation. In the central column, there is no transfer and in the right column, transfer is 'intrinsic-like'. (Color required for printed version).

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

We aimed to determine whether individual characteristics of participants could be linked to the magnitude of transfer from the dominant to the non-dominant arm. We first assessed the influence of handedness on sensorimotor adaptation, but no significant correlation was found between handedness and transfer value ($r=-0.22$; $p=0.35$); handedness did not significantly influence or correlate with any measure related to sensorimotor adaptation or transfer. 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 $= 0.1 \times$ 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
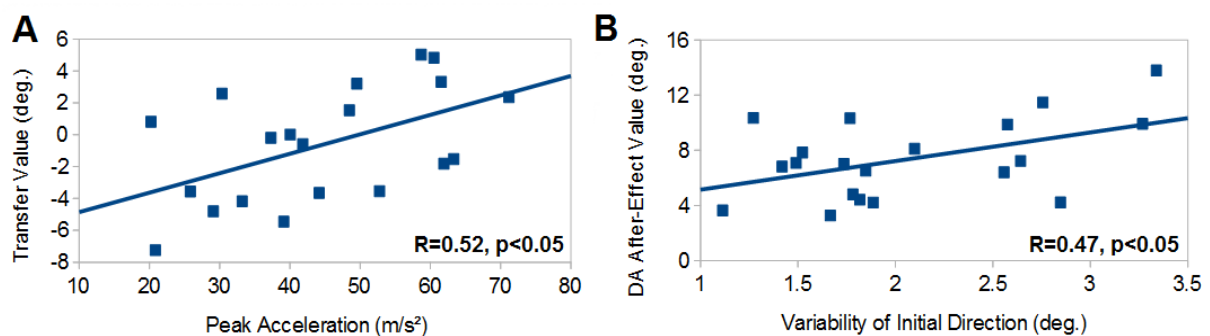
419

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 × PA + 2.28 × 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.
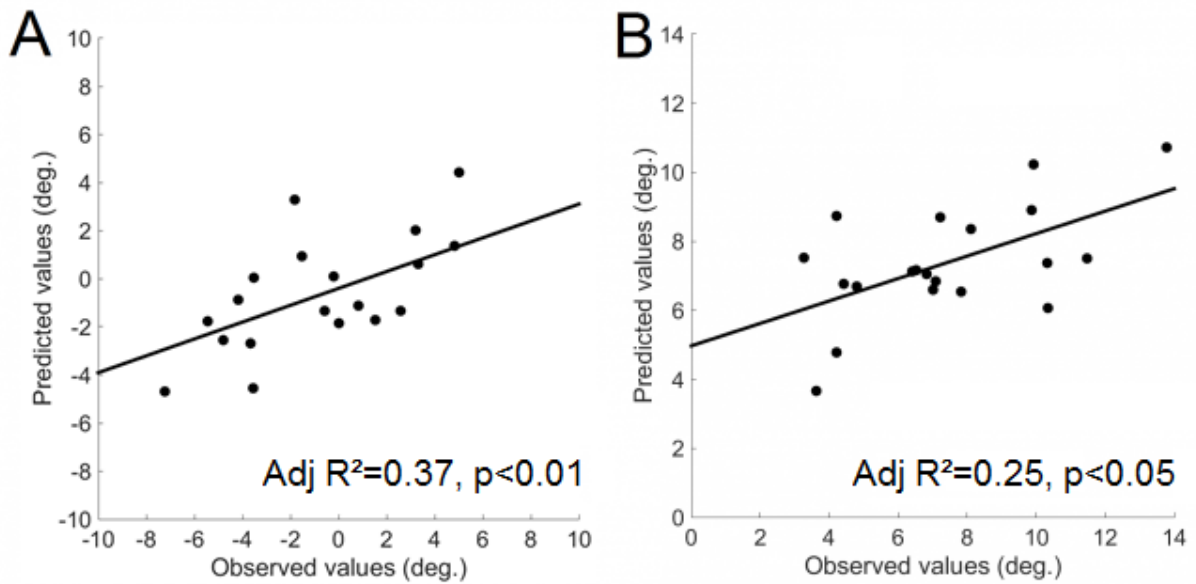
Figure 9: A/ Observed versus predicted transfer based on a multiple regression with two measures, peak acceleration across the Prism exposure phase and variability of initial direction in the late exposure phase (last 10 trials). B/ Observed versus predicted DA after-effect (absolute value), based on a multiple regression using variability of initial direction in late exposure and number of exposure trials to adapt. (Color not required for printed version).

We investigated a potential link between the transfer value and the after-effect value on the DA, but no significant correlation was found (r=-0.37; p=0.1). For the following analyses, we used the absolute value of the after-effect for clarity purposes (because all participants were deviated in the same direction during the DA POST-exposure 1st trial, so the greater the after-effect value, the more deviated to the left is the participant compared to his/her PRE-exposure phase). We found a positive linear correlation between variability of initial direction during the late exposure phase (last 10 trials) and the after-effect (Figure 8B; r=0.47; p=0.04). We also examined whether the magnitude of after-effect found on the DA could be correlated with kinematic data by using a multiple regression analysis, as we did for interlimb transfer. A forward-stepwise multiple regression revealed that late-exposure variability and the number of trials to adapt were the first two variables correlated with the 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 × variability - 0.35 ×

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 ± 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 ± 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 ± 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 ± 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 ± 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 ± 0.3). The 17 other participants assigned their trajectory errors to

483 external factors (mean score=8.4 ± 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 ± 5.1 deg.; mean of 17 participants reporting

486   'external factors' =-0.6 ± 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,

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

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

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

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

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

A parsimonious interpretation of these findings is that the way the new sensorimotor mapping was learned during exposure influenced subsequent movements, including those used to assess interlimb transfer. This is consistent with the idea that generalization of 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

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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