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Individual movement features during prism adaptation correlate with after-effects and interlimb transfer

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

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| 1 | Individual movement features during prism adaptation |
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| 2 | correlate with after-effects and interlimb transfer |
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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 \cong |
| 6 | |
| 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 |
| 10 | |
| 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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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

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 55 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 (He et al. 2016) did not confirm this correlation between motor variability and adaptation rate, it is currently hypothesized that motor variability may in part reflect active exploration of movement parameter space in order to optimize sensorimotor adaptation (Pekny et al. 2015; Therrien et al. 2016). Despite the body of work on these issues, the factors and mechanisms modulating generalization of sensorimotor adaptation remain unclear. Here we tested the hypothesis that specific kinematic characteristics of movements may be linked to the 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 adaptation more than movement velocity. 96

97 To facilitate the comparison between prismatic and force-field adaptation, we used the protocol and setup of Lefumat et al. (2015) but with a prismatic instead of dynamic 98 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.

117 Methods

118 Participants

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

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

131

132 Experimental setup

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

For the entire experiment, participants viewed the set-up and their arm binocularly through specific goggles which allowed vision only through the prism lenses (O'Shea et al. 2014). One set of goggles was standard (control) and the other was equipped with Fresnel 3M Press-on plastic lenses (3M Health Care, Specialties Division, St Paul, Minn., USA) as in Martin et al. (1996). The 30-diopter (~17 deg.) lenses were mounted base-left (thus producing
a rightward deviation of the visual field).

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



150

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

157

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 hand path. 1.6 s after trial onset, a 100-ms tone informed the participant to go back slowly to 165 166 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.

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

PRE-exposure phase (baseline): Participants executed 30 reaching movements with the
 dominant arm (DA) then 30 with the non-dominant arm (NDA) toward one of the three
 possible targets (10 trials per target for each hand). Trials toward the different targets were
 presented in a pseudorandom order which was similar for all 20 participants. When the
 PRE-adaptation phase was over, a 2-min break was given, goggles were removed and the
 control goggles previously worn by participants were discretely replaced with prismatic
 glasses. During the break, participants had to keep their eyes closed and stay motionless.

Prism exposure phase: Participants performed 100 movements with the dominant arm
 (DA) toward the central target (0 deg.) while wearing the prisms deviating the visual field
 by ~17 deg. to the right. At the end of this phase, a second 2-min break was given and
 prisms were replaced with control goggles by the experimenter. During the break,

184 participants kept their eyes closed and stayed motionless.

POST-exposure phase: Participants first executed 30 reaching movements with the nonexposed non-dominant arm (NDA), and then 30 movements with the dominant arm (DA) (10 trials per target for each hand). For both blocks, the first presented target was the central target (then target order was pseudo-randomised). For the NDA block, the second target presented was the right target and the third target was the left target. For the DA block, the second target presented was the left target and the third target was the right target.

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

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

Using Statistica 8 (StatSoft, Tulsa, OK, USA), repeated-measures analyses of variances
(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 participant was defined as the initial direction of the 1st trial made during the POST-exposure 244 245 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

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 ± 0.7 m/s). Most kinematic parameters did not substantially vary across the three phases of the session (PRE-exposure, 265 Prism exposure and POST-exposure) as ANOVAs showed no significant difference across 266 267 experimental phases (mean peak velocity across targets, arms and conditions= 3.1 ± 0.8 m/s, F(2,38)=0.1, p=0.87, η 2=0.007; time to peak velocity=154 ± 31 ms, F(2,38)=0.13, p=0.88, 268 269 η 2=0.005; peak acceleration =43.8 ± 16.4 m/s², F(2,38)=1.8, p=0.19, η 2=0.08; time to peak 270 acceleration=86 \pm 32 ms, F(2,38)=1.1, p=0.33, η 2=0.04; movement time=435 \pm 103 ms; 271 F(2,38)=2.7, p=0.08, η 2=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).

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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 the first trial was deviated to the right. Compared to the fast participants, slower participants had more time to visually compare hand and target positions and to correct for movement errors. This can be seen in Figure 2 which illustrates the motor behavior of two participants with different movement speeds. While all participants saw their hand going rightward with respect to the target, slower participants could adjust the arm trajectory during the course of 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] (PRE-exposure, Prism exposure 1st trial, 2nd trial, 3rd trial, 4th trial and 100th trial, POST-290 291 exposure 1st trial)] showed a significant effect of the experimental PHASE on initial 292 movement direction (F(6,114)=55.9, p=0.0000, η2=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.



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

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



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

317 exposure phase, and the 1^{st} 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).

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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).

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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: t(19)=0.45, p=0.66; Right target: t(20)=0.28, p=0.79). 363



365

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).

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 participant, we computed a 95% confidence interval from all movements made by each 373 374 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, transfer was not considered to be significant. When the initial direction of the first trial of 376 377 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 exhibited rightward (intrinsic-like) transfer and 4 participants exhibited no transfer: such 382 383 heterogeneity clearly appears on Figure 6B and Figure 7, which highlights the continuum of 384 interlimb transfer across participants.



386 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 387 388 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'. (Color 393 required for printed version).

385

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

396 *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 = $0.1 \times$ transfer value - 6; r=0.52; p=0.02). Low peak acceleration reflected a negative 412 413 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).

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

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 increased the percentage of explained variance (which reached 93% with 9 variables for 437 438 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).

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 1st 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; r=0.47; p=0.04). We also examined whether the magnitude of after-effect found on the DA 456 457 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 = $-5.03 + 1.91 \times$ 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 ± 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 \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

A classical pattern of prism adaptation was observed with the dominant arm: as in previous studies (Redding & Wallace 1988; Martin et al. 1996; Sarlegna et al. 2007; O'Shea et al. 2014), initial errors due to the prisms were reduced trial-by-trial and when prisms were removed, clear after-effects were observed with the trained limb. Such after-effects were observed after participants reached to the same central target as in the Prism exposure phase. After-effects were also observed on the two other lateral targets, consistent with previous reports of generalization of sensorimotor adaptation across movement directions for prism adaptation (Redding & Wallace 2006), visuomotor rotations (Ghahramani et al. 1996;
Krakauer et al. 2000) and adaptation to force fields (Thoroughman & Shadmehr 2000; Malfait
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 (Kakei et al. 1999; Kakei 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 heterogeneity. 556

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.

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

after-effects on the trained as well as the untrained arm. However, further work is necessaryto 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

In conclusion, 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 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

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651

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656

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- 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.
- and F.R.S. edited manuscript and approved the final version for submission.

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