



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

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Received: 5 April 2018 / Accepted: 16 October 2018
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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, Suy, Wenderoth, & Swinnen 2006; Taylor, Wojaczynski, Ivry 2011; Joiner, Braynov, Smith 2013; Mostafa, Salomonczyk, Cressman, Henriques 2014). Such effector-independent representation would underlie the interlimb transfer of sensorimotor adaptation, which also appears to be shaped by contextual conditions (Krakauer, Mazzoni, Ghazizadeh, Ravindran, Shadmehr 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, Kimura, Uka 1997). Indeed, Kitazawa et al. (1997) showed that when

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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, Miyamoto, Castro, Ölveczky, Smith 2014). Wu et al. (2014) reported that higher task-relevant motor variability during baseline was correlated with faster adaptation. While, 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 to optimize sensorimotor adaptation (Pekny, Izawa, Shadmehr 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.

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

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

perturbation. Although interlimb transfer of prism adaptation has sometimes been found to be non-significant (Kitazawa et al. 1997; Martin et al. 1996; Michel, Pisella, Prablanc, Rode, Rossetti 2007), we hypothesized based on several previous studies (Harris 1963; Cohen 1967; Cohen 1973; Taub & Goldberg 1973; Choe & Welch 1974; Wallace & Redding 1979) that interlimb transfer would be observed in the form of an after-effect on the first movement made after prismatic adaptation, without prisms, with the opposite, non-exposed arm. We reasoned that the presence of an after-effect would indicate the presence of interlimb transfer, but also that the direction of the after-effect would allow us to determine whether visuomotor adaptation is encoded in extrinsic or intrinsic coordinates (Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr 2003; Carroll, Poh, & de Rugy 2014; Stockinger, Thüerer, Focke, & Stein 2015). Specifically, when using prisms displacing the visual field rightward, encoding of dominant arm adaptation in extrinsic coordinates (associated with a leftward compensation) would predict a leftward after-effect on the non-dominant arm. In contrast, encoding in intrinsic coordinates (associated with shoulder and elbow abduction for instance) would predict a rightward after-effect. Lastly, because the degree of handedness has been shown to affect motor control and interlimb transfer (Chase & Seidler 2008; Sainburg 2014; Lefumat et al. 2015), we tested a mixed set of right- and left handers to provide a general model of interlimb transfer of prism adaptation.

Methods

Participants

Twenty young adults (13 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 12 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.

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° (straight-ahead), $+20^\circ$ (to the right) and -20° (to the left) with respect to start position.

For the entire experiment, participants viewed the setup 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 ($\sim 17^\circ$) 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 visual targets from an adjacent room using a customized software (Docometre) governing a real-time acquisition system (ADwin-Pro, Jäger, Lorsch, Germany).

Experimental procedure

At the beginning of each trial, participants had to actively position their specified (left or right) hand at the starting location (Fig. 1). They were asked to reach as fast and accurately as possible with their index finger toward the visual target, which was illuminated for 0.3 s. Participants were also instructed to 'reach in one movement' and not to

correct their position 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 the starting location. 7.4 s after trial onset, a 600-ms tone signalled to the participant that the trial had ended and that the next trial would start immediately. All participants were 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) to compare non-dominant arm performance just before and just after dominant arm performance with prisms. The experimental session consisted of three phases, as illustrated in Fig. 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°) while wearing the prisms deviating the visual field by $\sim 17^\circ$ 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, participants kept their eyes closed and stayed motionless.
- **POST-exposure phase:** Participants first executed 30 reaching movements with the non-exposed non-dominant

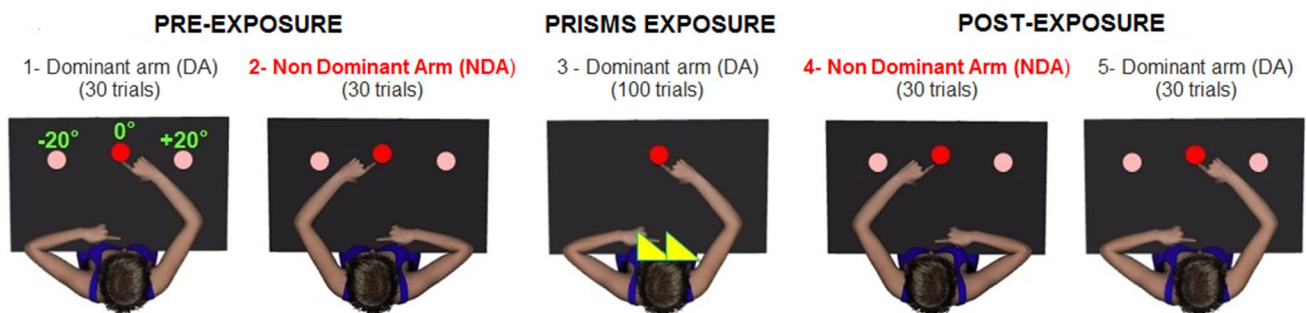


Fig. 1 Experimental conditions, illustrated with a right-handed participant. During the PRE-exposure phase, participants reached toward one of three visual targets with the dominant and the non-dominant arms. During the exposure phase, participants reached only toward

the central target with the dominant arm while wearing prisms. During the POST-exposure phase, participants reached toward one of three targets with the non-dominant arm and then with the dominant arm

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 infrared camera allowed continuous monitoring of participant's behavior. 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.

Because previous work suggested that interlimb transfer depends on the perceived source of motor errors (the credit-assignment issue; Berniker & Kording 2008), we aimed at directly assessing the assignment of motor errors and determine whether it could influence interlimb transfer. Immediately after the end of the reaching session, participants were asked open questions to determine whether they consciously perceived errors in movement trajectory during the first trials of the exposure phase. Then we showed a top view of each participant's arm trajectory in the first trial of the exposure phase and asked participants to fill a questionnaire. Participants were thus asked, in a counterbalanced order, 'Did you associate the errors you made early in the exposure phase to external factors?' and 'Did you associate the errors you made in the exposure phase to yourself (e.g., internal factors such as fatigue, inattention...)?'. Participants answered these two questions by placing a mark on a 10-cm 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.

Kinematic data analysis

Data, which are available upon request, were analyzed using Matlab (Mathworks, Natick, MA, USA). A few trials (0.9%) had to be discarded, because they were not properly performed by the participants or were corrupted by noise. Position data from the markers on the right and left index fingertips were low-pass filtered with a dual-pass, no-lag Butterworth (cut-off frequency: 8 Hz; order: 2). Movement onset was defined as the first-time hand velocity reached 3 cm/s and movement offset as the first-time hand velocity

dropped below 3 cm/s. Given that prisms mostly influence the direction of arm reaching movements, final movement accuracy was computed as the angle between the vector from the start position to the target position and the vector from the start position to the hand position at movement offset. Initial movement direction was computed as the angle between the vector from the start position to the target position and the vector from the start position to the hand position at peak velocity (Wang & Sainburg 2003). Since peak velocity occurred around 150 ms after movement onset in the present study, initial direction was considered the most critical dependant variable, because it mostly reflects the initial motor plan, before online visual feedback can substantially influence movement direction (Reichenbach, Franklin, Zatska-Haas, & Diedrichsen 2014; Sarlegna & Mutha 2015).

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 adaptation of the DA, the mean data of the ten movements toward the central target of the PRE-exposure phase (baseline) were compared with (1) the first trials and the last trial of the Prism exposure phase (to analyse the effect of the visual perturbation induced by prisms and the adaptation) and (2) the first trial of the POST-exposure phase (to analyse the after-effect). The number of trials to adapt was computed by comparing for each participant a 95% confidence interval of initial direction during the baseline PRE-exposure phase to the initial direction of the first movements made during the Exposure phase. We determined the number of trials which were necessary for initial direction during the Exposure phase to fall back 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 DA phase minus the mean of the initial direction of 10 trials made toward the central target during the PRE-exposure DA phase. We also assessed whether adaptation of DA movements toward the central target generalized across movement directions by comparing the mean data of the PRE-exposure movements toward one of the lateral targets to the value of the first trial in POST-exposure for the corresponding target.

To assess interlimb transfer of DA adaptation to the NDA, we compared the ten NDA movements toward the central target (0°) of the PRE-exposure phase to the first NDA movement of the POST-exposure phase (toward the central target). The transfer value of each participant was defined as the initial direction of the 1st trial made during the POST-exposure NDA phase minus the mean of the initial direction of 10 trials made toward the central target (0°) during the PRE-exposure NDA phase. All data had a normal

distribution as verified with the Kolmogorov–Smirnov method. Newman–Keuls tests were used for post-hoc analysis. For all tests, the significance threshold was set at 0.05.

Results

Prismatic adaptation of dominant arm movements

During the PRE-exposure experimental phase used to determine baseline performance, reaching movements were generally accurate (mean \pm SD final error = $0.3^\circ \pm 0.5^\circ$) 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, $F(2, 38) = 0.1$, $p = 0.87$, $\eta^2 = 0.007$; time to peak velocity = 154 ± 31 ms, $F(2, 38) = 0.13$, $p = 0.88$, $\eta^2 = 0.005$; peak acceleration = 43.8 ± 16.4 m/s², $F(2, 38) = 1.8$, $p = 0.19$, $\eta^2 = 0.08$; time to peak acceleration = 86 ± 32 ms, $F(2, 38) = 1.1$, $p = 0.33$, $\eta^2 = 0.04$; movement time = 435 ± 103 ms; $F(2, 38) = 2.7$, $p = 0.08$, $\eta^2 = 0.12$].

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 Fig. 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.

Adaptation was revealed by the reduction, trial after trial, of final errors as well as trajectory errors, which eventually became similar to baseline (Fig. 3, grey dots). Only the central target was used during the Prism exposure phase and when only considering 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-exposure 1st trial)] showed a significant effect of the experimental PHASE on initial movement direction [$F(6, 114) = 55.9$, $p = 0.0000$, $\eta^2 = 0.75$]. Post-hoc comparisons revealed that, as shown in Fig. 4a, initial direction was significantly deviated to the right for the first trial of the Prism exposure phase compared to baseline, i.e., to the mean of the ten movements toward the central target in the PRE-exposure phase; the shift was $+12.8^\circ$ on average across participants. Initial direction of the second and third movements of the Prism exposure phase also differed from baseline, but the initial direction of the fourth trial did not significantly differ from baseline, suggesting that it took about four trials for participants to adapt to the prism perturbation. When computed for each individual, the average number of trials for movements to fall back within

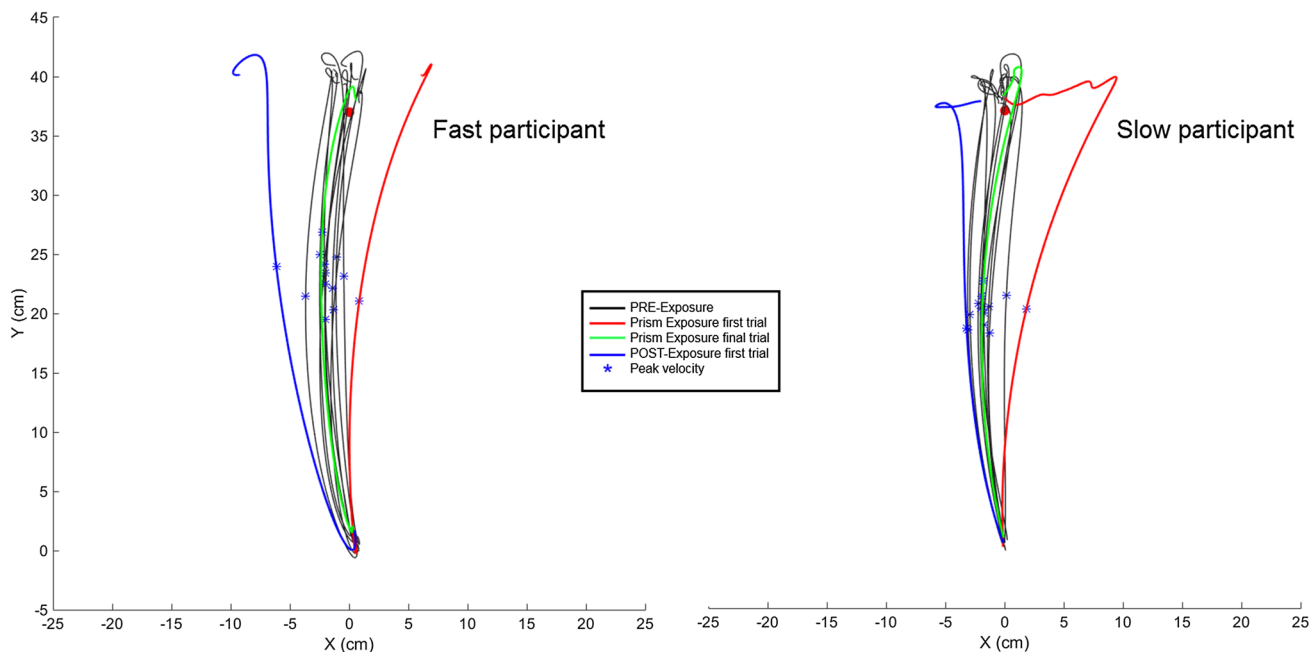


Fig. 2 Prism adaptation, illustrated with a top view of reaching movements with the dominant arm for a fast participant (mean peak velocity across the experiment = 3.9 m/s) and a slow participant (mean peak velocity across the experiment = 2.1 m/s)

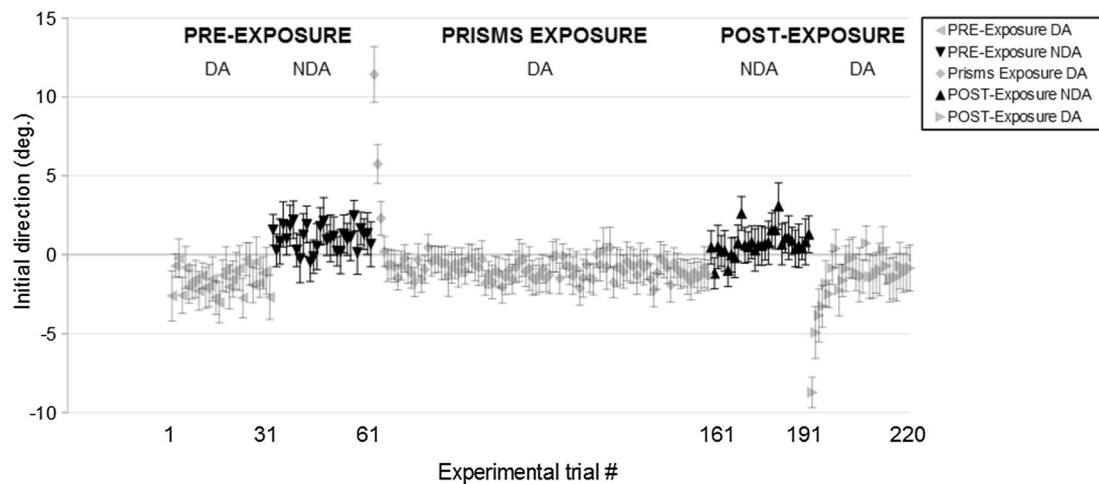


Fig. 3 Prism adaptation, illustrated with initial direction averaged across participants as a function of the experimental conditions. Error bars represent standard errors

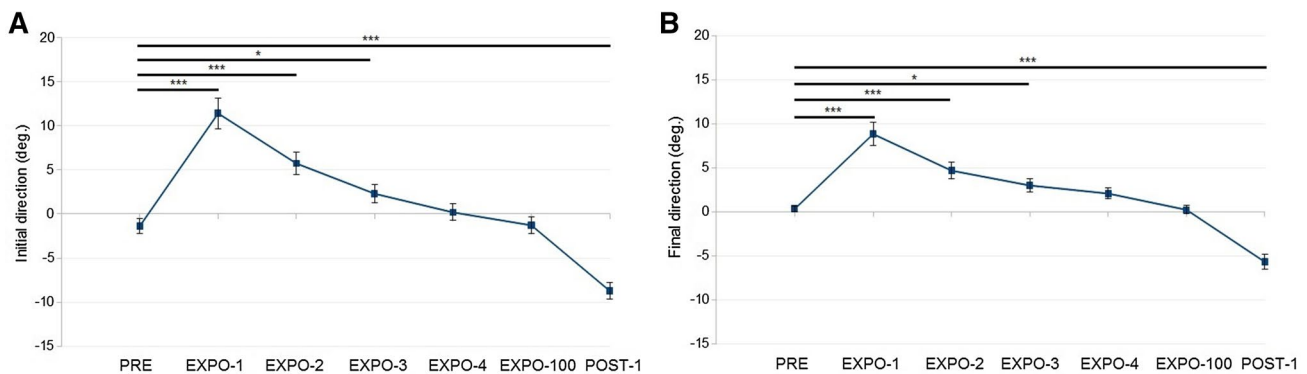


Fig. 4 Prism adaptation, illustrated with initial direction (**a**) and final direction (**b**) across experimental trials with the dominant arm. Data points represent the mean of ten trials toward the central target during PRE-exposure, the 1st, 2nd, 3rd, 4th and 100th trial of the Prism

exposure phase, and the 1st trial of the POST-Exposure phase. Error bars represent standard errors. * $p < 0.05$ *** $p < 0.001$, significant difference

the 95% confidence interval of the baseline was 4.7 ± 2.6 trials.

Prisms also influenced final reach accuracy (Fig. 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 [$F(6, 114) = 42.1, p = 0.0000, \eta^2 = 0.69$]. Final direction was deviated rightward on the first trial of the Prism exposure phase compared to baseline (the shift was $+8.5^\circ$ on average across participants). This analysis also suggests that adaptation occurred in about four trials.

After the Prism exposure phase, the rightward-deviating prisms were removed. Figures 2, 3, and 4 show that

following the POST-exposure phase testing the non-dominant arm, leftward after-effects were still observed on the dominant arm. Indeed, the first trial during the POST-exposure phase with the dominant arm was deviated to the left compared to the PRE-exposure phase (mean leftward shift in initial direction = 7.3° ; mean shift in final direction = 6.0°). The after-effect was systematic: when assessed for each participant by comparing initial direction in the first trial of POST-exposure to the 95% confidence interval of the baseline trials, the after-effect was significant for every single participant, further reflecting prism adaptation.

While reaching movements were made only toward the central target during the Prism exposure phase, different target directions were tested during the PRE- and the

POST-exposure phase to determine whether prism adaptation generalized across movement directions. Figure 5 shows that after-effects were also found for the lateral targets. A t test showed a significant difference between initial direction of the first DA movement toward the left target during the POST-exposure phase and the mean of the 10 trials made toward the left target during the DA PRE-exposure phase [$t(20)=3.07$; $p=0.006$; Cohen's $d=0.04$; see Fig. 5a]. An equivalent difference was seen for DA reaches to the right target [$t(20)=4.18$; $p=0.0005$; Cohen's $d=0.04$; see Fig. 5b]. These findings indicate generalization of prism adaptation across target directions. Such generalization was also statistically significant when analyzing final direction [for the left target: $t(20)=7.04$; $p=0.0000$; Cohen's $d=0.15$; and for the right target: $t(20)=3.74$; $p=0.001$; Cohen's $d=0.1$].

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 (Fig. 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: $t(20)=0.28$, $p=0.79$].

Interlimb transfer was not significant because of large inter-individual differences, as shown in Fig. 6a, b. 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' (Fig. 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 nine participants exhibited transfer in the leftward (extrinsic-like) direction, seven participants exhibited rightward (intrinsic-like) transfer and four participants exhibited no transfer: such heterogeneity clearly appears in Figs. 6b and 7, which highlights the continuum of interlimb transfer across participants.

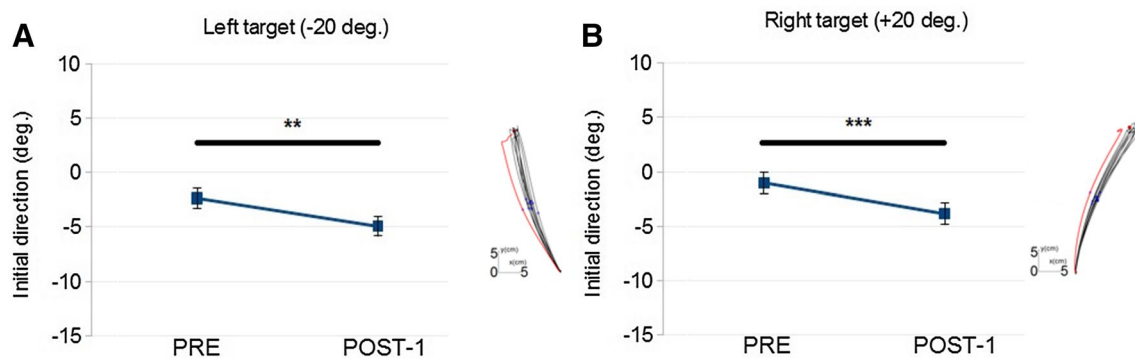


Fig. 5 Generalization of prism adaptation across movement directions, illustrated with initial direction of the dominant arm (DA) toward the left target (**a**) and right target (**b**) for the PRE-exposure phase (mean of ten trials) and the 1st trials of the POST-exposure phase toward the corresponding 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)

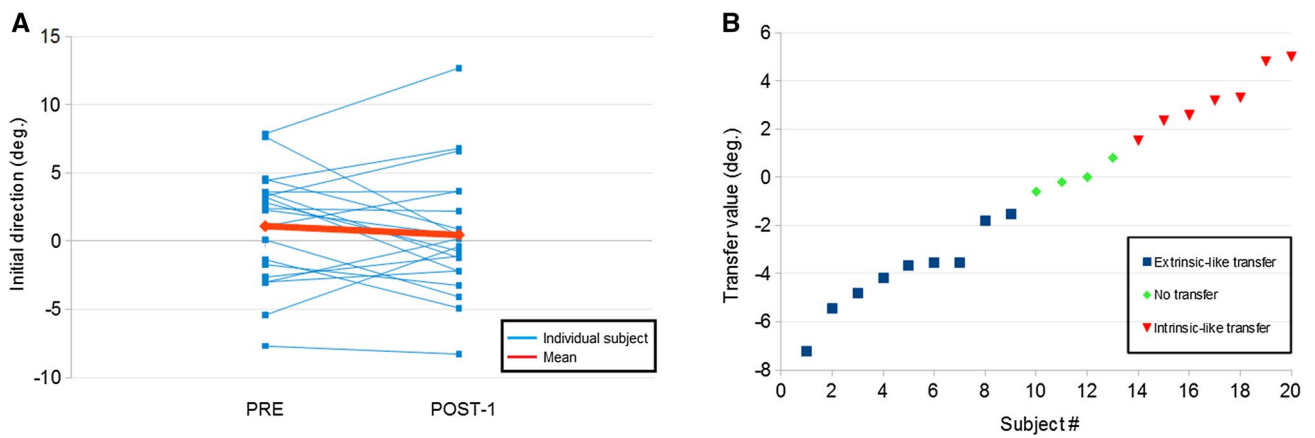


Fig. 6 **a** Initial direction of each participant with the non-dominant arm (blue lines) across the PRE-exposure phase (mean of ten trials) and for the 1st trial of the POST-exposure phase. The mean initial direction across all participants is in red line. **b** Transfer value (POST-1 – PRE) of each participant

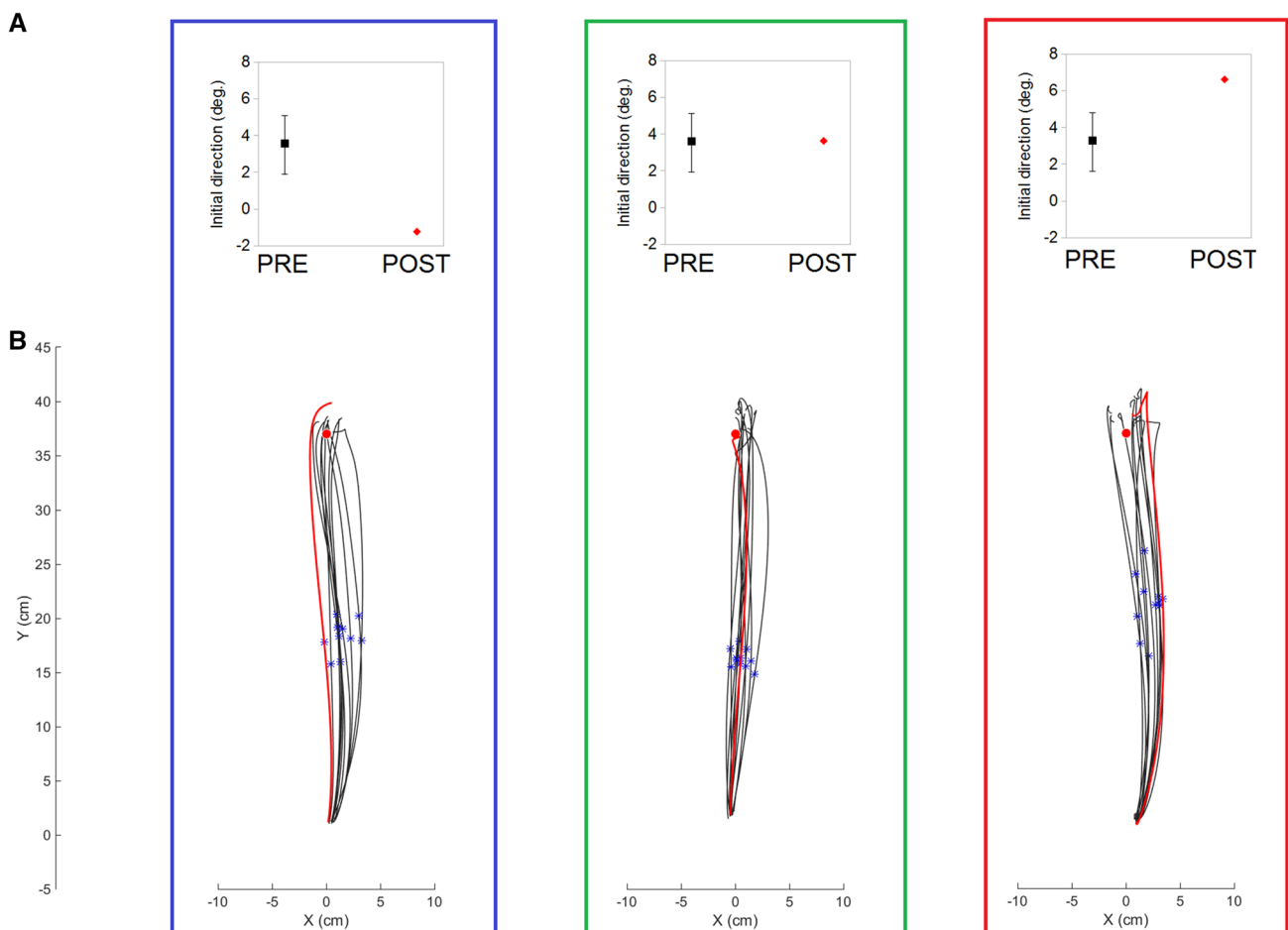


Fig. 7 Examples of interlimb transfer for three participants. **a** 95% confidence intervals built from PRE-exposure data (black), contrasted with the first trial of the POST-exposure phase (red). **b** Top views of reaching movements with the non-dominant arm during the PRE-exposure phase (black lines) 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’

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, previous work suggested that movement variability and velocity could influence sensorimotor adaptation (Kitazawa et al. 1997; Wu et al. 2014; Pekny et al. 2015; Lefumat et al. 2015; Therrien et al. 2016) and also distinguished the early and late phases of adaptation in terms of underlying mechanisms (Smith, Ghazizadeh, Shadmehr 2006; Wolpert, Diedrichsen, Flanagan 2011). We thus investigated the influence of peak velocity, peak acceleration and variable trajectory errors throughout adaptation or specifically during the early and late phases of Prism exposure (first and last ten exposure trials). We found that interlimb transfer was correlated with variables typically associated to movement vigor, such as peak acceleration and peak velocity (Mazzoni, Hristova, & Krakauer 2007; Reppert et al. 2018). Figure 8a shows a positive linear correlation between the transfer value and the mean peak acceleration averaged across the Prism exposure phase ($PA = 0.1 \times \text{transfer value} - 6$; $r = 0.52$; $p = 0.02$). Low peak acceleration corresponded to a negative transfer value (Fig. 8a) and, therefore, extrinsic transfer, while high peak acceleration corresponded to a positive transfer value and, therefore, intrinsic transfer. As expected across the Prism exposure phase, peak acceleration was correlated with peak velocity ($r = 0.96$; $p = 0.0000$). Peak velocity was also positively correlated with the transfer value ($r = 0.48$; $p = 0.03$).

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

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 ten trials) and the after-effect (Fig. 8b, $r = 0.47$; $p = 0.04$). We also examined whether the magnitude of after-effect found

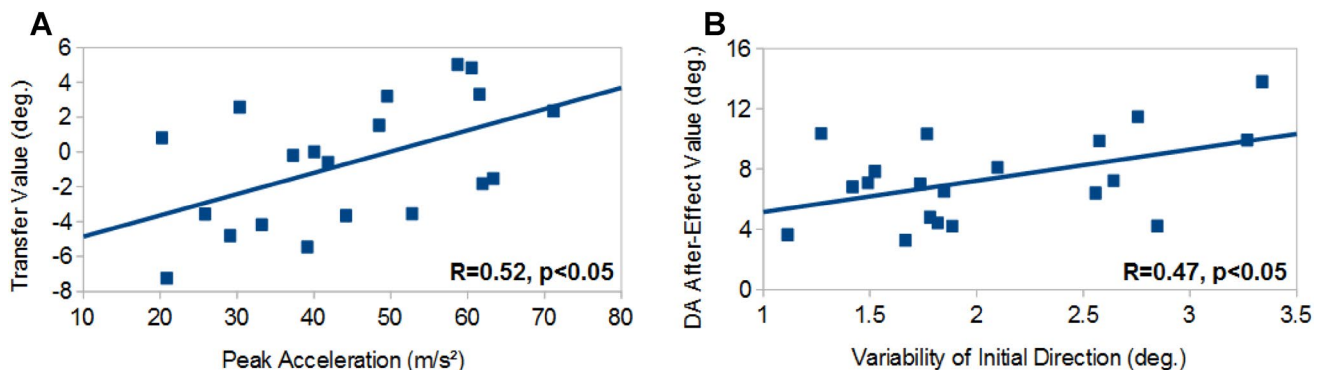


Fig. 8 **a** Correlation between interlimb transfer and mean peak acceleration averaged across the prism exposure phase. **b** Correlation between DA after-effect and variability of initial direction of the ten last trials of the prism exposure phase

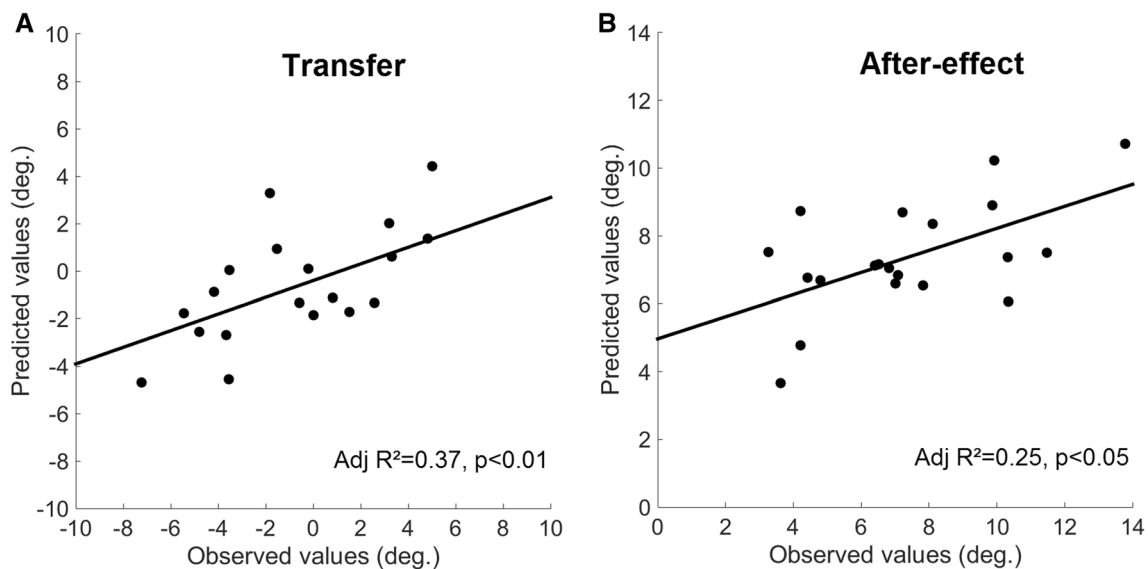


Fig. 9 a Observed versus predicted transfer based on a multiple regression with two measures, peak acceleration across the Prism exposure phase and variability of initial direction in the late exposure phase (last ten trials). **b** Observed versus predicted DA after-effect

on the DA could be correlated with kinematic data 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 regression equation was: absolute after-effect value = $-5.03 + 1.91 \times \text{variability} - 0.35 \times \text{number of trials}$, indicating that the greater the variability and the fewer trials needed to adapt, the greater the after-effect. Figure 9b shows the relationship between the observed and the predicted after-effect values based on the equation of the multiple regression.

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

Only one participant answered that he was not consciously aware of the errors made during the beginning of the exposure phase, although his initial direction was shifted by 6.5° compared to his baseline. When asked whether they associated their errors to external factors, participants tended to agree (mean score 8.0 ± 2.3 with 10 indicating ‘strongly agree’). When asked whether they associated the errors they made in the exposure phase to themselves, participants tended to disagree (mean score 2.7 ± 3.0). When participants had to report whether they assigned trajectory errors to ‘internal factors’ (0) or ‘external factors’ (10), they tended to assign their errors to external factors (mean score 7.8 ± 2.2).

(absolute value), based on a multiple regression using variability of initial direction in late exposure and number of exposure trials to adapt

No significant correlation was found between the transfer value and the assignment of errors (all $r < 0.08$; all $p > 0.51$).

With respect to the question ‘internal factors’ or ‘external factors’, only three of the participants pointed toward ‘internal factors’ (mean score 4.1 ± 0.8). When these three participants were asked ‘Did you associate the errors you made in the exposure phase to yourself?’, all of them agreed (mean score 7.0 ± 1.4). These three participants did not agree when asked ‘Did you associate the errors you made early in the Exposure phase to external factors?’ (mean score 3.4 ± 0.3). The 17 other participants assigned their trajectory errors to external factors (mean score 8.4 ± 1.6). A Mann–Whitney non-parametric test showed that the transfer value did not significantly depend on the assignment of errors (mean of three participants reporting ‘internal factors’ = $-1.0^\circ \pm 5.1^\circ$; mean of 17 participants reporting ‘external factors’ = $-0.6^\circ \pm 3.5^\circ$; $p = 0.71$).

Discussion

We aimed to test the hypothesis that specific features of movements can influence the interlimb transfer of sensorimotor adaptation. We used a well-known visuomotor perturbation (prismatic glasses) to induce sensorimotor adaptation and assessed generalization across directions and interlimb transfer (Harris 1963; Martin et al. 1996; Kitazawa et al. 1997; Morton & Bastian 2004; Michel et al. 2007). Prisms have been used to study the process of visuomotor adaptation, since the pioneering work of von Helmholtz (1867)

and Stratton (1896) and the acquired knowledge has been valuable, for instance for the rehabilitation of strabismus or spatial neglect (Rossetti et al. 1998). For the practical purpose of personalized training (Seidler et al. 2015) as well as for a better understanding of the factors which influence transfer of sensorimotor adaptation, we re-investigated the interlimb transfer of prism adaptation with detailed analyses of movement kinematics for each individual.

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, Gauthier, & Blouin 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, Wolpert, & Jordan 1996; Krakauer, Pine, Ghilardi, & Ghez 2000) and adaptation to force fields (Thoroughman & Shadmehr 2000; Malfait, Shiller, & Ostry 2002; Lefumat et al. 2015).

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

Interlimb transfer of prismatic adaptation

To determine whether sensorimotor adaptation is limb specific, a classic test is to determine whether adaptation with one arm influences the opposite arm. As early as 1963, Harris reported that interlimb transfer of prism adaptation was limited. In the present study, interlimb transfer was not significant at the group level and a large heterogeneity across participants was uncovered. This appears to be consistent with the heterogeneity of findings in the literature. At an individual level, we found that for some of the participants

($N=4$), there was no interlimb transfer of prism adaptation, in line with the overall finding in several previous studies (Kitazawa et al. 1997; Martin et al. 1996; Michel et al. 2007). For other participants ($N=9$), interlimb transfer was observed in the form of leftward after-effects on the non-dominant arm, which could reflect the leftward compensation of the rightward prism deviation, in extrinsic or visual space (Harris 1963; Cohen 1967; Cohen 1973; Taub & Goldberg 1973; Choe & Welch 1974; Wallace & Redding 1979). However, a second, intrinsic coordinate system can be considered (Criscimagna-Hemminger et al. 2003; Galea, Miall, & Woolley 2007; Wiestler, Waters-Metenier, & Diedrichsen 2014; Franklin, Batchelor, & Wolpert 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, Ivry, & Mangun 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, Press, & Smith 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 (Takei, Hoffman, & Strick 1999; Takei, Hoffman, & Strick 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 & Kording 2009). An alternative hypothesis is that there is a possible link between the speed/acceleration of a movement and the nature of its neural representation. This may be related to the idea that faster movements mostly rely on feedforward control, because less time is available to process peripheral sensory feedback during movement execution. Feedforward motor control describes how motor neurons control muscles without using sensory feedback, most likely with signals in an intrinsic, muscle-based coordinate system (Tanaka & Sejnowski 2013). Slower movements can be controlled with online feedback to adjust the hand path, and the importance of visual feedback in human movement control has been highlighted (Reichenbach et al. 2014; Sarlegna & Mutha 2015). The fact that visual feedback control relies on the use of signals originally in extrinsic, retina-based coordinates, may be related to the encoding of slower visually guided movements in extrinsic coordinates. Hence, our findings suggest that movement vigor could explain the heterogeneity of interlimb transfer reported in previous prism adaptation studies, in which unfortunately movement speed or acceleration was rarely reported.

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

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

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 encoding of

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

Author contributions AGR, HL, J-LV, LB and FRS designed the experiment; AGR, HL and FRS performed experiments; AGR and FRS analyzed data; AGR prepared figures; AGR, HL, J-LV, RCM, LB, CB and FRS interpreted results of experiments; AGR and FRS drafted manuscript; AGR, HL, J-LV, RCM, LB, CB and FRS edited manuscript and approved the final version for submission.

Funding This work was supported by Aix-Marseille University (International Relations Grant), the Royal Society (International Travel Grant), the CNES (APR Grants) and the CNRS (PICS, DEFISENS and AUTON programs). The funders had no role in study design, data collection and analysis.

Conflict of interest The authors declare no competing financial interests.

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

Informed consent Informed consent was obtained from all individual participants included in the study.

References

- Alexander, M. S., Flodin, B. W., & Marigold, D. S. (2011). Prism adaptation and generalization during visually guided locomotor tasks. *Journal of Neurophysiology*, *106*(2), 860–871.
- Berniker, M., Franklin, D. W., Flanagan, J. R., Wolpert, D. M., & Kording, K. (2014). Motor learning of novel dynamics is not represented in a single global coordinate system: Evaluation of mixed coordinate representations and local learning. *Journal of Neurophysiology*, *111*(6), 1165–1182.
- Berniker, M., & Kording, K. (2008). Estimating the sources of motor errors for adaptation and generalization. *Nature Neuroscience*, *11*(12), 1454.
- Brayanov, J. B., Press, D. Z., & Smith, M. A. (2012). Motor memory is encoded as a gain-field combination of intrinsic and extrinsic action representations. *Journal of Neuroscience*, *32*(43), 14951–14965.
- Carroll, T. J., Poh, E., & de Rugy, A. (2014). New visuomotor maps are immediately available to the opposite limb. *Journal of Neurophysiology*, *111*(11), 2232–2243.
- Chase, C., & Seidler, R. (2008). Degree of handedness affects intermanual transfer of skill learning. *Experimental Brain Research*, *190*(3), 317–328.
- Choe, C. S., & Welch, R. B. (1974). Variables affecting the intermanual transfer and decay of prism adaptation. *Journal of Experimental Psychology*, *102*(6), 1076.
- Cohen, M. M. (1967). Continuous versus terminal visual feedback in prism aftereffects. *Perceptual and Motor Skills*, *24*(3), 1295–1302.
- Cohen, M. M. (1973). Visual feedback, distribution of practice, and intermanual transfer of prism aftereffects. *Perceptual and Motor Skills*, *37*(2), 599–609.
- Criscimagna-Hemminger, S. E., Donchin, O., Gazzaniga, M. S., & Shadmehr, R. (2003). Learned dynamics of reaching movements generalize from dominant to nondominant arm. *Journal of Neurophysiology*, *89*(1), 168–176.
- DiZio, P., & Lackner, J. R. (1995). Motor adaptation to Coriolis force perturbations of reaching movements: Endpoint but not trajectory adaptation transfers to the nonexposed arm. *Journal of Neurophysiology*, *74*(4), 1787–1792.
- Donchin, O., Rabe, K., Diedrichsen, J., Lally, N., Schoch, B., Gizevski, E. R., & Timmann, D. (2012). Cerebellar regions involved in adaptation to force field and visuomotor perturbation. *Journal of Neurophysiology*, *107*(1), 134–147.
- Faisal, A. A., Selen, L. P., & Wolpert, D. M. (2008). Noise in the nervous system. *Nature Reviews Neuroscience*, *9*(4), 292.
- Franklin, D. W., Batchelor, A. V., & Wolpert, D. M. (2016). The sensorimotor system can sculpt behaviorally relevant representations for motor learning. *eNeuro*, *3*(4), ENEURO-E0070.
- Galea, J. M., Miall, R. C., & Woolley, D. G. (2007). Asymmetric interlimb transfer of concurrent adaptation to opposing dynamic forces. *Experimental Brain Research*, *182*(2), 267–273.
- Gazzaniga, M. S., Ivry, R. B., & Mangun, G. R. (1998). *Cognitive neuroscience: The biology of the mind*. New York: WW Norton & Co.
- Ghahramani, Z., Wolpert, D. M., & Jordan, M. I. (1996). Generalization to local remappings of the visuomotor coordinate transformation. *Journal of Neuroscience*, *16*(21), 7085–7096.
- Haith, A., & Vijayakumar, S. (2009). Implications of different classes of sensorimotor disturbance for cerebellar-based motor learning models. *Biological Cybernetics*, *100*(1), 81–95.
- Hamilton, C. R. (1964). Intermanual transfer of adaptation to prisms. *The American Journal of Psychology*, *77*(3), 457–462.
- Harris, C. S. (1963). Adaptation to displaced vision: Visual, motor, or proprioceptive change? *Science*, *140*(3568), 812–813.
- Hay, L., & Brouchon, M. (1972). Analysis of reorganization of visuomotor coordination in humans. Generalization of adaptation to prismatic deviation of the visual space. *L'annee psychologique*, *72*(1), 25–38.
- Held, R., & Freedman, S. J. (1963). Plasticity in human sensorimotor control. *Science*, *142*(3591), 455–462.
- Herzfeld, D. J., & Shadmehr, R. (2014). Motor variability is not noise, but grist for the learning mill. *Nature Neuroscience*, *17*(2), 149.
- He, K., Liang, Y., Abdollahi, F., Bittmann, M. F., Kording, K., & Wei, K. (2016). The statistical determinants of the speed of motor learning. *PLoS Computational Biology*, *12*(9), e1005023.
- Joiner, W. M., Brayanov, J. B., & Smith, M. A. (2013). The training schedule affects the stability, not the magnitude, of the interlimb transfer of learned dynamics. *Journal of Neurophysiology*, *110*(4), 984–998.

- Takei, S., Hoffman, D. S., & Strick, P. L. (1999). Muscle and movement representations in the primary motor cortex. *Science*, 285(5436), 2136–2139.
- Takei, S., Hoffman, D. S., & Strick, P. L. (2001). Direction of action is represented in the ventral premotor cortex. *Nature Neuroscience*, 4(10), 1020.
- Kalil, R. E., & Freedman, S. J. (1966). Intermanual transfer of compensation for displaced vision. *Perceptual and Motor Skills*, 22(1), 123–126.
- Kanai, R., & Rees, G. (2011). The structural basis of inter-individual differences in human behaviour and cognition. *Nature Reviews Neuroscience*, 12(4), 231.
- Kitazawa, S., Kimura, T., & Uka, T. (1997). Prism adaptation of reaching movements: Specificity for the velocity of reaching. *Journal of Neuroscience*, 17(4), 1481–1492.
- Krakauer, J. W., Mazzoni, P., Ghazizadeh, A., Ravindran, R., & Shadmehr, R. (2006). Generalization of motor learning depends on the history of prior action. *PLoS Biology*, 4(10), e316.
- Krakauer, J. W., Pine, Z. M., Ghilardi, M.-F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *Journal of Neuroscience*, 20(23), 8916–8924.
- Lefumat, H. Z., Miall, R. C., Cole, J. D., Bringoux, L., Bourdin, C., Vercher, J.-L., & Sarlegna, F. R. (2016). Generalization of force-field adaptation in proprioceptively-deafferented subjects. *Neuroscience Letters*, 616, 160–165.
- Lefumat, H. Z., Vercher, J.-L., Miall, R. C., Cole, J., Buloup, F., Bringoux, L., Bourdin, C., & Sarlegna, F. R. (2015). To transfer or not to transfer? Kinematics and laterality quotient predict interlimb transfer of motor learning. *Journal of Neurophysiology*, 114(5), 2764–2774.
- Malfait, N., & Ostry, D. J. (2004). Is interlimb transfer of force-field adaptation a cognitive response to the sudden introduction of load? *Journal of Neuroscience*, 24(37), 8084–8089.
- Malfait, N., Shiller, D. M., & Ostry, D. J. (2002). Transfer of motor learning across arm configurations. *Journal of Neuroscience*, 22(22), 9656–9660.
- Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996). Throwing while looking through prisms: II. Specificity and storage of multiple gaze—throw calibrations. *Brain*, 119(4), 1199–1211.
- Mattar, A. A., & Ostry, D. J. (2010). Generalization of dynamics learning across changes in movement amplitude. *Journal of Neurophysiology*, 104(1), 426–438.
- Mazzoni, P., Hristova, A., & Krakauer, J. W. (2007). Why don't we move faster? Parkinson's disease, movement vigor, and implicit motivation. *Journal of Neuroscience*, 27(27), 7105–7116.
- McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. *Trends in Cognitive Sciences*, 20(7), 535–544.
- Michel, C., Pisella, L., Prablanc, C., Rode, G., & Rossetti, Y. (2007). Enhancing visuomotor adaptation by reducing error signals: Single-step (aware) versus multiple-step (unaware) exposure to wedge prisms. *Journal of Cognitive Neuroscience*, 19(2), 341–350.
- Morton, S. M., & Bastian, A. J. (2004). Prism adaptation during walking generalizes to reaching and requires the cerebellum. *Journal of Neurophysiology*, 92(4), 2497–2509.
- Mostafa, A. A., Salomonczyk, D., Cressman, E. K., & Henriques, D. Y. (2014). Intermanual transfer and proprioceptive recalibration following training with translated visual feedback of the hand. *Experimental Brain Research*, 232(6), 1639–1651.
- O'Shea, J., Gaveau, V., Kandel, M., Koga, K., Susami, K., Prablanc, C., & Rossetti, Y. (2014). Kinematic markers dissociate error correction from sensorimotor realignment during prism adaptation. *Neuropsychologia*, 55, 15–24.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Parmar, P. N., Huang, F. C., & Patton, J. L. (2015). Evidence of multiple coordinate representations during generalization of motor learning. *Experimental Brain Research*, 233(1), 1–13.
- Pekny, S. E., Izawa, J., & Shadmehr, R. (2015). Reward-dependent modulation of movement variability. *Journal of Neuroscience*, 35(9), 4015–4024.
- Redding, G. M., & Wallace, B. (1988). Components of prism adaptation in terminal and concurrent exposure: Organization of the eye-hand coordination loop. *Perception & Psychophysics*, 44(1), 59–68.
- Redding, G. M., & Wallace, B. (2006). Generalization of prism adaptation. *Journal of Experimental Psychology: Human Perception and Performance*, 32(4), 1006.
- Reichenbach, A., Franklin, D. W., Zatka-Haas, P., & Diedrichsen, J. (2014). A dedicated binding mechanism for the visual control of movement. *Current Biology*, 24(7), 780–785.
- Reppert, T. R., Rigas, I., Herzfeld, D. J., Sedaghat-Nejad, E., Komogortsev, O., & Shadmehr, R. (2018). Movement vigor as a traitlike attribute of individuality. *Journal of Neurophysiology*, 120(2), 741–757.
- Rossetti, Y., Rode, G., Pisella, L., Farné, A., Li, L., Boisson, D., & Perenin, M.-T. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, 395(6698), 166.
- Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization. *Frontiers in Psychology*, 5, 1092.
- Sarlegna, F. R., & Bernier, P. M. (2010). On the link between sensorimotor adaptation and sensory recalibration. *Journal of Neuroscience*, 30(35), 11555–11557.
- Sarlegna, F. R., Gauthier, G. M., & Blouin, J. (2007). Influence of feedback modality on sensorimotor adaptation: Contribution of visual, kinesthetic, and verbal cues. *Journal of Motor Behavior*, 39(4), 247–258.
- Sarlegna, F. R., & Mutha, P. K. (2015). The influence of visual target information on the online control of movements. *Vision Research*, 110, 144–154.
- Seidler, R. D., Mulavara, A. P., Bloomberg, J. J., & Peters, B. T. (2015). Individual predictors of sensorimotor adaptability. *Frontiers in Systems Neuroscience*, 9, 100.
- Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biology*, 4(6), e179.
- Stockinger, C., Thüerer, B., Focke, A., & Stein, T. (2015). Intermanual transfer characteristics of dynamic learning: Direction, coordinate frame, and consolidation of interlimb generalization. *Journal of Neurophysiology*, 114(6), 3166–3176.
- Stratton, G. M. (1896). Some preliminary experiments on vision without inversion of the retinal image. *Psychological Review*, 3(6), 611.
- Sun, Z. Y., Pinel, P., Rivière, D., Moreno, A., Dehaene, S., & Mangin, J.-F. (2016). Linking morphological and functional variability in hand movement and silent reading. *Brain Structure and Function*, 221(7), 3361–3371.
- Tanaka, H., & Sejnowski, T. J. (2013). Computing reaching dynamics in motor cortex with Cartesian spatial coordinates. *Journal of Neurophysiology*, 109(4), 1182–1201.
- Taub, E., & Goldberg, I. A. (1973). Prism adaptation: Control of intermanual transfer by distribution of practice. *Science*, 180(4087), 755–757.
- Taylor, J. A., Wojaczynski, G. J., & Ivry, R. B. (2011). Trial-by-trial analysis of intermanual transfer during visuomotor adaptation. *Journal of Neurophysiology*, 106(6), 3157–3172.
- ten Donkelaar, H. J., Lammens, M., Wesseling, P., Hori, A., Keyser, A., & Rotteveel, J. (2004). Development and malformations

- of the human pyramidal tract. *Journal of Neurology*, 251(12), 1429–1442.
- Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2016). Effective reinforcement learning following cerebellar damage requires a balance between exploration and motor noise. *Brain*, 139(1), 101–114.
- Thoroughman, K. A., & Shadmehr, R. (2000). Learning of action through adaptive combination of motor primitives. *Nature*, 407(6805), 742.
- Vangheluwe, S., Suy, E., Wenderoth, N., & Swinnen, S. P. (2006). Learning and transfer of bimanual multifrequency patterns: Effector-independent and effector-specific levels of movement representation. *Experimental Brain Research*, 170(4), 543–554.
- Von Helmholtz, H. (1867). *Handbuch der physiologischen Optik*, vol. 9. New York: Voss.
- Wallace, B., & Redding, G. M. (1979). Additivity in prism adaptation as manifested in intermanual and interocular transfer. *Perception and Psychophysics*, 25(2), 133–136.
- Wang, J., & Sainburg, R. L. (2003). Mechanisms underlying interlimb transfer of visuomotor rotations. *Experimental Brain Research*, 149(4), 520–526.
- Wei, K., & Kording, K. (2009). Relevance of error: What drives motor adaptation? *Journal of Neurophysiology*, 101(2), 655–664.
- Wiestler, T., Waters-Metenier, S., & Diedrichsen, J. (2014). Effector-independent motor sequence representations exist in extrinsic and intrinsic reference frames. *Journal of Neuroscience*, 34(14), 5054–5064.
- Wolpert, D. M., Diedrichsen, J., & Flanagan, J. R. (2011). Principles of sensorimotor learning. *Nature Reviews Neuroscience*, 12(12), 739.
- Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P., & Smith, M. A. (2014). Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nature Neuroscience*, 17(2), 312.

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