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**RESEARCH ARTICLE** | *Control of Movement*

# Transfer of dynamic motor skills acquired during isometric training to free motion

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**Melendez-Calderon A, Tan M, Bittmann MF, Burdet E, Patton JL.** Transfer of dynamic motor skills acquired during isometric training to free motion. *J Neurophysiol* 118: 219–233, 2017. First published March 29, 2017; doi:10.1152/jn.00614.2016.—Recent studies have explored the prospects of learning to move without moving, by displaying virtual arm movement related to exerted force. However, it has yet to be tested whether learning the dynamics of moving can transfer to the corresponding movement. Here we present a series of experiments that investigate this isometric training paradigm. Subjects were asked to hold a handle and generate forces as their arms were constrained to a static position. A precise simulation of reaching was used to make a graphic rendering of an arm moving realistically in response to the measured interaction forces and simulated environmental forces. Such graphic rendering was displayed on a horizontal display that blocked their view to their actual (statically constrained) arm and encouraged them to believe they were moving. We studied adaptation of horizontal, planar, goal-directed arm movements in a velocity-dependent force field. Our results show that individuals can learn to compensate for such a force field in a virtual environment and transfer their new skills to the actual free motion condition, with performance comparable to practice while moving. Such nonmoving techniques should impact various training conditions when moving may not be possible.

**NEW & NOTEWORTHY** This study provided early evidence supporting that training movement skills without moving is possible. In contrast to previous studies, our study involves *1*) exploiting cross-modal sensory interactions between vision and proprioception in a motionless setting to teach motor skills that could be transferable to a corresponding physical task, and *2*) evaluates the movement skill of controlling muscle-generated forces to execute arm movements in the presence of external forces that were only virtually present during training.

motor learning; motor adaptation; visual feedback; isometric

WE PLAN, EXECUTE, AND LEARN new movements by integrating information from different sensory modalities and our previous experience of the environment. The difference between predicted and actual sensory consequences of movement — one form of error — allows us to adapt and update our actions (Takiyama et al. 2015). How much we adapt our movements from such errors depends on the ability of the central nervous system (CNS) to recognize familiar errors and make use of recent experiences (Herzfeld et al. 2014); we learn more from persistent errors than from persistent changes in the system. When our CNS receives conflicting sensory information between sensory modalities — another form of error — the CNS needs to understand what caused such discrepancy to make sense of the environment (Berniker and Kording 2008) — credit assignment problem — and learn performing actions in it. If there is unreliable or inconsistent feedback, it is generally accepted that the CNS combines available sensory information based on its perceived reliability and prior experience to resolve error information (Ernst and Banks 2002; Körding and Wolpert 2004).

Sensory information can be incorporated into the motor plan or neglected by CNS depending on its perceived relevance to the context in which the information is obtained. For example, when subjects perform point-to-point reaching movements under a force field with visual information about the extent of the movement, while lacking visual information about the lateral deviation from the straight line to the target, subjects did not compensate for the field (Scheidt et al. 2005). One interpretation of this study is that the conflicting sensory information between vision and proprioception hampered adaptation; another interpretation can be that proprioceptive information was irrelevant to achieve the goal of the task. This latter interpretation is backed up by a second experimental group performed by Scheidt et al. (2005) and by Franklin et al. (2007), who observed that, when the context-relevant visual feedback was removed completely during reaching movements, subjects could still adapt to the force field. Another example on the importance of context-relevant feedback is given by Franklin and Wolpert (2008). In their experiment, Franklin and Wolpert observed that conflicting visual feedback affected the trajectory of reaching movements only when the visual information was "task relevant," meaning that the conflicting information was maintained until the end of the movement. Indeed, context-relevant feedback can be so deceptive to the CNS that different groups have been able to create the perception of distance, size, displacement, mass, stiffness, and even texture by modifying only the visual information pro-

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vided (Dominjon et al. 2005; Lecuyer 2009; Lecuyer et al. 2010). These studies have shown that the CNS can be "tricked" to perceive physical properties that do not actually exist.

If movement adaptation and environment perception can be influenced by conflicting, yet context-relevant, sensory information, can we exploit such mechanisms to teach movement skills in the absence of motion? Our hypothesis is that, if the CNS has a sensor-independent representation of movements, which results from combining information from different sensory modalities, it should then be possible to learn from a sensor-independent error signal and transfer those skills to a task in which all sensory information is available, as long as the feedback is context relevant. In this regard, this study investigates the extreme case of training a dynamic movement in isometric conditions — isometric training — by creating a synesthetic illusion (Biocca et al. 2001) of movement and evaluates the transfer of skills to the corresponding dynamic task in free motion. During isometric training, not only is proprioception arising from muscle spindles not veridical, but other mechanoreceptors that can include Golgi tendon organs and even skin sensors are all different from that of the real motion condition. Thus it is unclear whether isometric training would transfer to the corresponding task or would result in poorly performing movement patterns. However, we believe that there exists a domain of generalization where muscle contraction sequences and visual information sufficiently overlaps with reality during the isometric condition, which would allow for sufficient generalization and transfer.

Several previous studies involved learning in isometric conditions (e.g., Liu et al. 2006; Mah and Mussa-Ivaldi 2003; Rotella et al. 2015; Todorov et al. 1997); however, they did not test whether and how the learned motor skills in the isometric scenario would transfer to actual movements. In contrast, our study *1*) involves exploiting the adaptive processes in a motionless setting to teach motor skills that could be transferable to a corresponding physical task and *2*) evaluates movement skill of controlling/adapting to internal and external forces that were only virtually present during training.

## METHODS

### *Participants*

Thirty-seven right-handed subjects in their twenties to thirties participated in these experiments. Seven subjects participated in *experiment 1* (see *Experiment 1: Evaluation*), while thirty participated in *experiment 2* (see *Experiment 2: Verification*).

To participate in this study, participants had to be at least 21 yr of age and had no physical or mental disorders that would prevent completion of the experimental protocol. All subjects provided consent in accordance with Northwestern University and the Rehabilitation Institute of Chicago. All participants were naive to the experimental procedures.

### *Experimental Setup*

We studied horizontal, planar, goal-directed arm movements in a velocity-dependent force field. Similar dynamic environments have been well studied within the motor control community (e.g., Brashers-Krug et al. 1996; Conditt et al. 1997; Flanagan et al. 1999; Franklin et al. 2003; Shadmehr and Mussa-Ivaldi 1994) and is thus an excellent reference to test this technique.

Participants were seated in a chair of adjustable height to accommodate individual requirements. Their dominant hand, with forearm in pronation, was attached to the end point of a two degree of freedom (2-DOF) manipulandum (or robot) using bandages. A wrist support prevented wrist movements, while an arm support attached to the subject's forearm kept the arm in horizontal position and cancelled the influence of gravity. A 2-DOF force sensor (Assurance Technologies, Bartlett, IL) was located at the point of attachment between the robot's end point and the handle, directly below the palm of the hand.

The participants' arms were occluded by a horizontal screen. A realistic graphic rendering of an arm, with similar subject-specific anatomical characteristics (i.e., arm lengths and position of centers of rotation relative to the subjects' seat position) — an "avatar arm" — was displayed on the screen (Fig. 1). With such realistic visual feedback, we aimed at creating a strong illusion among participants that they were looking at their actual arm throughout the experiment.

A 0.5-cm diameter cursor was overlaid on the top of the avatar's hand. Participants were required to move the cursor from a 1-cm-diameter origin toward three randomly appearing, 1-cm-diameter targets oriented at 120° from each other.

During the free motion condition, the avatar's movements matched the participants' actual arm movements while moving the manipulandum. During the isometric condition, the robot's end-effector was clamped with a stiff, physical brake so that participants could not move their arm; the avatar's movements were determined by the forces that subjects applied against the robot handle and animated using "virtual" dynamic environments (see APPENDIX). The experimenter could manually switch between free motion and isometric conditions in less than 10 s.

Throughout the experiments, participants experienced different dynamic environments in both free and isometric conditions:

- Dynamic environments in free motion condition

–Real null field (**rNF**): free motion, no external forces were applied.

–Real force field (**rVF**): a velocity-dependent force F (N) was applied by the robot to the subject's hand according to

$$\vec{F} = \begin{bmatrix} 0 & 25 \\ -25 & 0 \end{bmatrix} \dot{\vec{X}} \qquad (1)$$

where $\dot{\vec{X}}$ s the subject's hand velocity.

- Dynamic environments in the isometric condition

–Virtual null field (**vNF**): Subjects' movements were constrained by a physical brake. The force exerted to the manipulandum's handle moved the avatar according the equations of motion presented in the APPENDIX.

–Virtual force field (**vVF**): Similar to vNF, with the addition of a velocity-dependent field *(Eq. 1)* to the modeled arm dynamics.

### *Experiment 1: Evaluation*

Seven subjects were asked to perform center-out movements to three targets that were 10 cm from the origin and oriented at 120° from each other. A trial started when subjects either left the origin or the cursor speed was greater than 0.04 m/s. To advance to the next trial, subjects were asked to return to the origin. Depending on the experimental phase, movements from origin to target were perturbed by a force field (real or virtual). Target-to-origin movements were uninstructed and never perturbed by a force field. The presentation of the targets was randomized such that no movement would repeat more than twice in a row.

Feedback about the movement duration was provided after each trial with a text on the screen indicating whether the movement was "too slow" (above 0.7 s, target also turned blue), "too fast" (below 0.5 s, target turned red) or in the desired range (between 0.5 s and 0.7 s, target turned green). Additionally, if the movement was performed within the required time range and the maximum perpendicular error (defined as the perpendicular distance between the cursor and the line

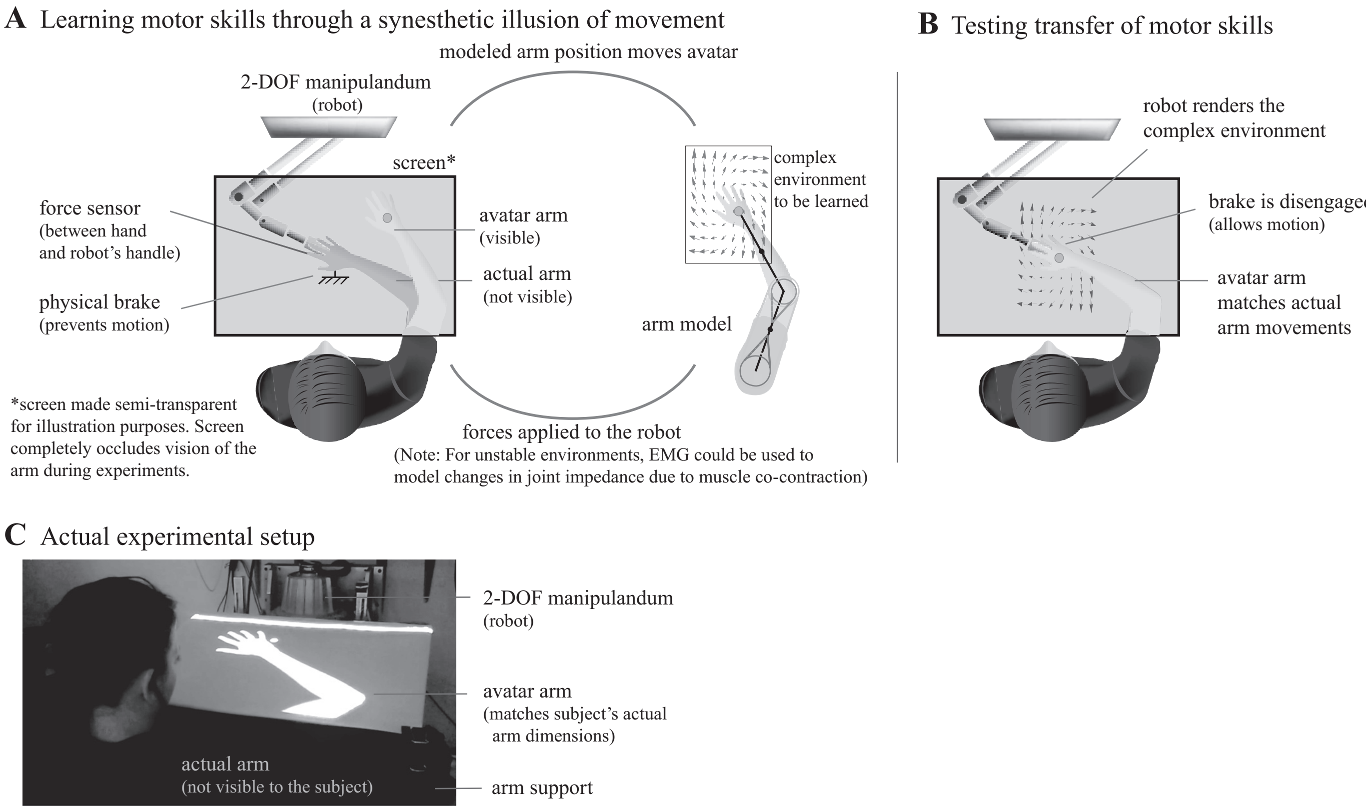


Fig. 1. A diagram showing the physical layout of the experimental space. *A*: the isometric condition of the experiment, where the avatar arm moves based on forces applied by the subject. The subject's true arm is clamped so that it remains stationary. *B*: the free motion condition, the virtual arm model moves with the arm, such that the virtual arm always overlaps with the subject's true arm. *C*: actual look of the experimental condition, where a realistic virtual arm is displayed.

connecting the origin with the target) was below 3 cm, the system indicated "Perfect" and the screen's background became green for a few seconds. These feedback mechanisms were implemented to ensure the average speeds of movement remained relatively constant (since applied forces depended on movement speed) and to encourage subjects to perform straight movements.

The experimental protocol consisted of five phases in an isometric condition followed by six phases in a free motion condition (see Fig. 2). Partial results of this experiment were presented in the conference proceedings (Melendez-Calderon et al. 2015). In this article, we present an updated analysis to (Melendez-Calderon et al. 2015) to be consistent with the methodology used in *experiment 2*, without invalidating previous findings.

### *Experiment 2: Verification*

The goal of *experiment 2* was to test whether the observed results of *experiment 1* would hold after elimination of possible confounding factors in *experiment 1*. Thirty healthy right-handed subjects were randomly assigned to one of three different groups in equal numbers:

- *Transfer effects rVF* (G1): Subjects trained movements in an isometric condition under vVF and their performance in rVF in free motion was tested immediately after the training session.
- *Transfer effects rNF* (G2): Subjects trained movements in an isometric condition under vVF and their performance in rNF in free motion was tested immediately after the training session.
- *Control* (G3): Subjects trained movements in free motion under rVF; their performance in rVF and rNF was tested immediately after the training session. This group was never exposed to the isometric condition.

Subjects were asked to perform center-out movements to three targets that were 15 cm from the origin (5 cm longer than in *experiment 1*) and oriented at 120° from each other. In contrast to *experiment 1*, subjects were asked to remain in the target after completing the movement and perform a target-to-origin movement, which was also perturbed by a force field for some of the experimental phases, to prevent deadaptation during these movements. Data from

| Phase | Name | Condition | Dynamic environment | # of trials per direction (# catch trials per direction) |
|---|---|---|---|---|
| 1 | Familiarization | Isometric | vNF | 5 |
| 2 | Before-effects | | vNF (vVF catch trials) | 28 (7) |
| 3 | Training (Isometric) | | vVF | 50 |
| 4 | After-effects | | vVF (vNF catch trials) | 28 (7) |
| 5 | Refresher | | vVF | 3 |
| Experimenter pauses the experiment and disengages the brake (~30 s) | | | | |
| 6 | Transfer-effects | Free motion | rVF | 3 |
| 7 | Transfer-effects | | rVF (rNF catch trials) | 12 (3) |
| 8 | Training (Free motion) | | rVF | 20 |
| 9 | After-effects | | rVF (rNF catch trials) | 28 (7) |
| 10 | Washout | | rNF | 5 |
| 11 | Post-washout | | rNF (rVF catch trials) | 28 (7) |

Fig. 2. *Experiment 1*: Protocol. Intermittent catch trials, where a dynamic environment is suddenly changed, are indicated with parentheses.

target-to-origin movements was not considered in statistical analysis, to keep consistency with experiment 1.

Even though movements in *experiment 2* were longer than in *experiment 1*, we still expected subjects to perform movements within 0.6 s. The rationale for this was to make the external forces stronger and the task more challenging than *experiment 1*. Such increase in difficulty would result in an increased magnitude of the errors. If subjects are able to able to adapt to this more challenging environment, then the evidence for isometric training approach would be more apparent.

To have better control over the consistency of movement speeds, feedback about the movement speed was provided after each trial. Assuming a minimum-jerk movement, we have a desired hand speed peak of

$$\dot{x}_{peakDesired} = 1.875 * movementLength\ [m] / movementTime\ [s]$$
$$\dot{x}_{peakDesired} = 0.468\ \ [m/s] \qquad (2)$$

After each trial, the system indicated (without text as in *experiment 1*) whether the trial was too slow (hand speed peak 15% lower than $\dot{x}_{peakDesired}$, i.e., $< 0.398$ m/s, target turned blue), too fast (hand speed peak 15% higher than $\dot{x}_{peakDesired}$, i.e., $> 0.539$ m/s, target turned red), or within the required peak speed range (target turned green), to ensure the average peak speeds of movement remained relatively constant since applied forces depended on movement speed. In addition, the screen's background turned green if the movement was within the required peak speed and with low perpendicular error ($<3$ cm, as in *experiment 1*).

For the transfer effects groups, the experimental protocol consisted of three phases in free motion to identify baseline performance, followed by three phases in isometric, where subjects were familiarized to the isometric condition and exposed to vVF; the experiment finished by an additional phase in free motion to evaluate the transfer effects. For the *control* group, the experiment protocol was similar, except that subjects were not exposed to isometric but remained in free motion for the whole experiment. Details of the experimental protocol are summarized in Fig. 3.

*Data Analysis*

*Outcome measures.* Different measures of directional error during force-field paradigms have been used extensively to quantify adaptation and feedforward control (Casadio et al. 2007; Donchin et al. 2003; Schabowsky et al. 2007; Smith and Shadmehr 2005; Thoroughman and Shadmehr 2000). In our study, we quantified directional error, defined in detail in the APPENDIX. This measure can be used as an indicator of the trajectory "straightness" that resulted from feedforward control commands. It is a "signed" measure and can thus identify biases to either side of the desired movement direction. In addition, we quantified gross lateral movement corrections by the number of times the velocity profile, along the axis perpendicular to the line connecting the origin and the target, changed sign and reached at least 25% of the peak speed. The calculation of movement corrections excluded the corrections performed during stabilization, once the subject reached the target.

*Outliers.* Outliers were removed from the data sets before any statistical tests. We considered trials that indicated anticipation to the appearance of the target on the screen as outliers. To identify anticipation to the target appearance, we look at the exit angle after movement initiation. This corresponds to the angle that is formed between the line joining the cursor position at movement onset and the center of the target and the line tangent to the cursor position at 50 ms after movement onset. We considered that subjects were anticipating a movement to another direction if a trial had an exit angle lower than $-60°$ or higher than $60°$ as illustrated in Fig. 4.

*Statistical analysis.* For statistical analysis, we conducted an unrestricted least significant difference procedure. Data from each subject and each experimental phase was first checked for normality using a Shapiro-Wilk test. All directional error data passed the normality test; thus multiple *t*-tests or paired *t*-tests were performed. For analysis of lateral movement corrections we used Mann-Whitney tests (for nonpaired data) and Wilcoxon signed-rank tests (for paired data). Given the observational nature of our study, the main purpose of these multiple comparisons was not to simultaneously generate and test hypotheses, but rather to discern interesting differences that can be

| | | | Group | | | | Group | |
|---|---|---|---|---|---|---|---|---|
| | | | *Transfer-effects rVF* | *Transfer-effects rNF* | | | *Control* | |
| **Phase** | **Name** | **Condition** | **Dynamic environment** | | **# of trials / direction (# catch trials / direction)** | **Condition** | **Dynamic environment** | **# of trials / direction (# catch trials / direction)** |
| 1 | Familiarization | Free motion | rNF | | 2 | Free motion | rNF | 2 |
| 2 | Baseline | Free motion | rNF | | 5 | Free motion | rNF | 5 |
| 3 | Pre-training | Free motion | rNF (rVF catch trials) | | 20 (5) | Free motion | rNF (rVF catch trials) | 20 (5) |
| | | Experimenter pauses the experiment and engages the brake (~30 s) | | | | Experimenter pauses the experiment and pretends to do something with the robot (~30 s) | | |
| 4 | Familiarization | Isometric | vNF | | 2 | Free motion | rNF | 2 |
| 5 | Baseline | Isometric | vNF | | 5 | Free motion | rVF | 5 |
| 6 | Training | Isometric | vVF | | 50 | Free motion | rVF | 45 |
| | | Experimenter pauses the experiment and disengages the brake (~30 s) | | | | Experimenter pauses the experiment and pretends to do something with the robot (~30 s) | | |
| 7 | Post-training | Free motion | rVF | NA | 5 | Free motion | rVF | 5 |
| | | Free motion | | | | Experimenter pauses the experiment and pretends to do something with the robot (~30 s) | | |
| 8 | Post-training | Free motion | NA | rNF | 5 | Free motion | rNF | 5 |

Fig. 3. *Experiment 2*: Protocol. Intermittent catch trials, where a dynamic environment is suddenly changed, are indicated with parentheses.

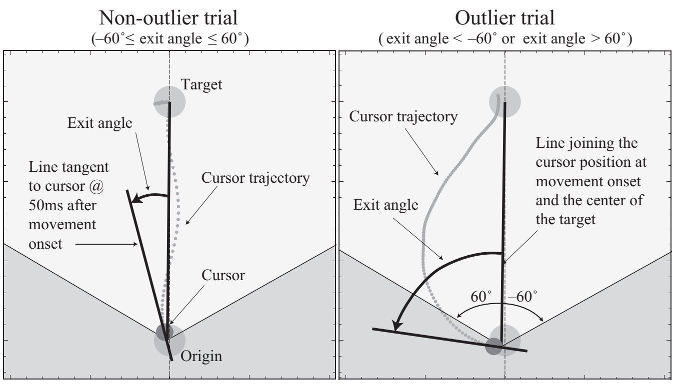


Fig. 4. Example of a nonoutlier and an outlier trial based on exit angle criterion.

tested more rigorously in subsequent studies. Therefore, the reported $P$ values should be seen as "an indication as to which of the observed differences are likely to be real" (Saville 1990) and not necessarily as a solid statistical proof. In the figures, one asterisk (*) represents statistical significance at $P \leq 0.05$, two asterisks (**) at $P \leq 0.01$, and three asterisks (***) at $P \leq 0.001$.

Whisker box plots were chosen to examine the spread of the data. Each box shows the distance between two quartiles surrounding the median, and lower boundary line indicate the max[1st quartile−1.5*IQR, min(data)], while the upper boundary line indicate min[3rd quartile + 1.5*IQR, max(data)]. A diamond indicates the sample mean, with end points spanning at 95% confidence interval (CI) for the sample mean.

The reported mean CIs for paired differences are based on Student's $t$-distribution with (number of subjects−1) degrees of freedom; whereas the CIs of difference of means from independent groups consider 2*(number of subjects per group−1) degrees of freedom. The CI for difference in medians from independent groups was estimated by the Hodges-Lehmann method.

## RESULTS

### *Experiment 1*

Figure 5 shows the raw movement trajectories of the seven unimpaired subjects that participated in this study. All subjects adapted and compensated for the virtual force field in the isometric condition, as measured by a decrease in directional errors. For the comparisons described below, please refer to Fig. 6.

Cursor movements in isometric under the influence of a virtual force field (vVF) were much straighter after isometric training than before the training: comparison $\mathbf{A_1}$ (2 vs. 3*) [95% CI $\mu_{(3*-2)} = 29.34 \pm 2.77°$; paired $t$-test, $P < 0.001$]. Movements after training were no different than movements in isometric without a force field (i.e., vNF) prior to training: comparison $\mathbf{B_1}$ (1 vs. 3*) [95% CI $\mu_{(3*-1)} = -2.08 \pm 3.63°$; paired $t$-test, $P = 0.21$).

The acquired motor skills after isometric training partially transferred to the free motion condition. Comparison $\mathbf{C_1}$ (6 vs. 11) shows a statistically significant difference between movements in free motion with a real force field (rVF) immediately following the isometric training and unexpected rVF movements after a washout period at the end of the experiment [95% CI $\mu_{(11-6)} = -6.41 \pm 1.58°$; paired $t$-test, $P < 0.001$]. This suggests that subjects were able to compensate for the real force field in free motion after the isometric training. However, other comparisons suggest that these skills were only partially transferred. Directional errors of movements of intermittent trials in free motion when the real force field was unexpectedly turned off, i.e., aftereffect movements, were not statistically different after isometric training than after free motion training: comparison $\mathbf{D_1}$ (7 vs. 9) [95% CI $\mu_{(9-7)} = 2.32 \pm 3.19°$; paired $t$-test, $P = 0.12$). However, after training rVF in free motion, subjects compensated for the real force field slightly

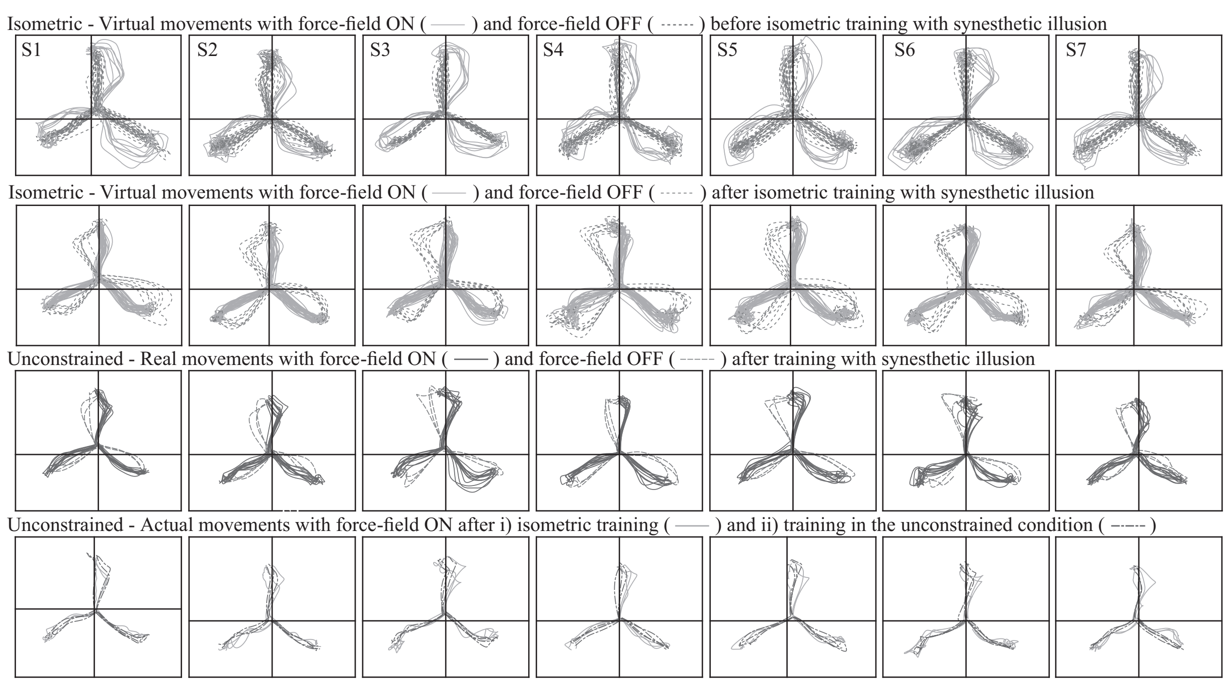


Fig. 5. Movement trajectories of subjects participating in *experiment 1*. Subjects performed point-to-point (virtual) reaching movements in isometric and unconstrained conditions. All subjects learned to compensate for a velocity-dependent field by training with a synesthetic illusion of movement, i.e., isometric training.

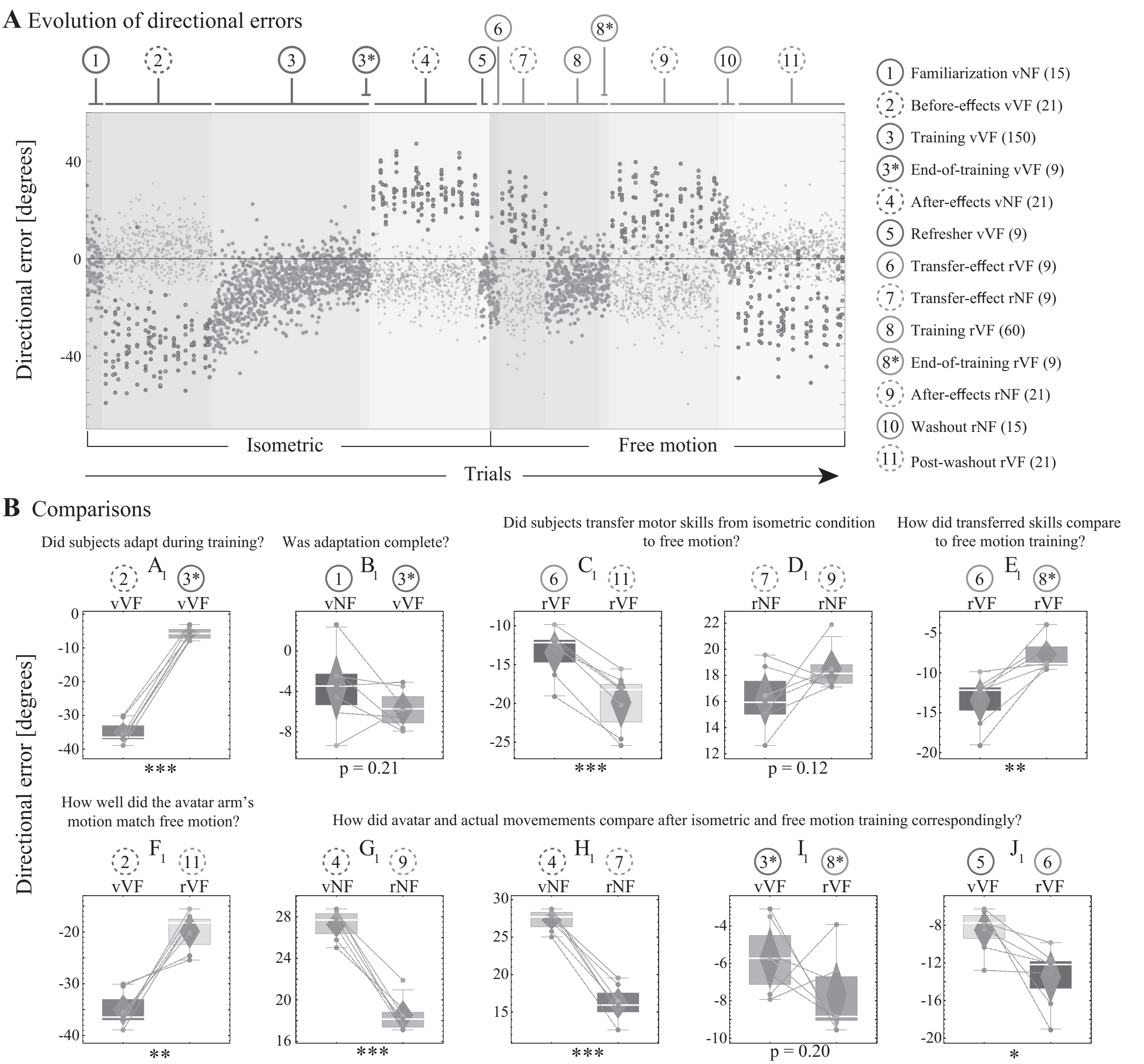


Fig. 6. *A*: directional errors during the different experimental phases of *experiment 1*. Note that the phases 3* and 8* correspond to the final trials of the phases 3 and 8, respectively. Each dot represents the directional error of a trial. Different dot colors represent different subjects. Phases indicated by dashed circles had intermittent catch trials, within these phases, noncatch trials are represented by smaller dimmer dots. *B*: comparison of different phases. Different dot colors represent the mean (without considering far outliers) of each subject within a specific experimental phase. $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

better than after training in isometric: comparison $\mathbf{E_1}$ (6 vs. 8*) [95% CI $\mu_{(8*-6)} = 5.77 \pm 3.00°$; paired *t*-test, $P < 0.001$].

The difference in comparison $\mathbf{E_1}$ indicates that the learned motor commands after isometric training are not totally equivalent to those learned after free motion training. While this can be attributed to several factors (e.g., incomplete adaptation, sudden congruency between visual and proprioceptive feedback, maladaptation of internal representation of limb state), there is some indication that inaccuracies in the modeled arm dynamics could have also played a role. Comparison $\mathbf{F_1}$ (2 vs. 11) shows that the effects of an unexpected force field on the arm movements are greater on the simulated arm than on the real one [95% CI $\mu_{(11-2)} = 15.19 \pm 6.47°$; paired *t*-test, $P < 0.01$]. While the lower directional errors on phase 11 could also be attributed to the fact that this phase was sampled at the end of the experiment, similar effects were also observed between virtual and real movements when the force field was unexpectedly turned off after a training phase. Movement deviations were greater on the simulated arm after isometric training than deviations produced by the actual arm after unconstrained training: comparison $\mathbf{G_1}$ (4 vs. 9) [95% CI $\mu_{(9-4)} = -8.75 \pm 2.02°$; paired *t*-test, $P < 0.001$]; comparison $\mathbf{H_1}$ (4 vs. 7) [95% CI $\mu_{(7-4)} = -11.08 \pm 2.12°$; paired *t*-test, $P < 0.001$].

Regardless of the possible effects introduced by model inaccuracies, subjects moved similarly (visually) straight in vVF and rVF after its corresponding training phase: comparison $\mathbf{I_1}$ (3* vs. 8*) [95% CI $\mu_{(8*-3*)} = -1.97 \pm 3.37°$; paired *t*-test, $P = 0.20$). However, the force commands that allow the simulated arm to move straight did not produce such straight movements when actually moving in a force field: comparison $\mathbf{J_1}$ (5 vs. 6) [95% CI $\mu_{(6-5)} = -4.96 \pm 4.06°$; paired *t*-test, $P < 0.05$]. Therefore, it is likely that our model had underestimated the arm mass, joint impedance, or intrinsic feedback mechanisms.

### *Experiment 2*

The results of *experiment 1* suggest that the idea of training movement skills without moving actually works. However, one could argue that the observed transfer effects in *experiment 1* could have been influenced by the exposure to the actual dynamic environment by measuring rNF transfer effects with intermittent exposure to rNF within rVF trials. *Experiment 2* aimed at removing this conflicting factor by having two groups, one in which we tested transfer effects in rVF and the other transfer effects in rNF, without the use of catch trials. The results from *experiment 2* further support the findings of *experiment 1*. For the comparisons described below, please refer to Fig. 7.

Subjects from the transfer effect groups (G1 and G2) were able to adapt and compensate for virtual force field (vVF) in the isometric condition. Cursor movements in isometric condition with a virtual force field (vVF) were straighter at the end than at the beginning of the training phase: comparison $\mathbf{A_2}$ ($6^b_{G1}$ vs. $6^e_{G1}$) [95% CI $\mu_{(6^e_{G1}-6^b_{G1})} = 23.18 \pm 2.33°$; paired *t*-test, $P < 0.001$]; comparison $\mathbf{B_2}$ ($6^b_{G2}$ vs. $6^e_{G2}$) [95% CI $\mu_{(6^e_{G2}-6^b_{G2})} = 18.03 \pm 5.34°$; paired *t*-test, $P < 0.001$]. Similarly, subjects in the *control* group (G3) adapted to the force field in free motion: comparison $\mathbf{C_2}$ ($6^b_{G3}$ vs. $6^e_{G3}$) [95% CI $\mu_{(6^e_{G3}-6^b_{G3})} = 14.33 \pm 5.13°$; paired *t*-test, $P < 0.001$].

Similar to the findings in *experiment 1*, the acquired motor skills in isometric training were partially transferred to the free motion condition. For the *transfer effects rVF* group (G1), movements in free motion with rVF after isometric training were *1*) straighter than intermittent trials in rVF before the training: comparison $\mathbf{D_2}$ ($3_{G1}$ vs. $7^b_{G1}$) [95% CI $\mu_{(7^b_{G1}-3_{G1})} = 22.20 \pm 7.00°$; paired *t*-test, $P < 0.001$]; and *2*) as straight as movements performed by the *control* group (G3) after free motion training: comparison $\mathbf{E_2}$ ($7^b_{G1}$ vs. $7^b_{G3}$) [95% CI $\mu_{(7^b_{G3})}-\mu_{(7^b_{G1})} = -2.76 \pm 7.18°$; *t*-test, $P = 0.42$). For the *transfer effects rNF* group (G2), directional errors of movements in free motion with rNF after isometric training were *1*) more skewed than baseline trials in rNF before the training: comparison $\mathbf{F_2}$ ($2_{G2}$ vs. $8^b_{G2}$) [95% CI $\mu_{(8^b_{G2}-2_{G2})} = 11.33 \pm 5.90°$; paired *t*-test, $P < 0.01$]; and *2*) as skewed as rNF movements by the *control* group (G3) after free motion training: comparison $\mathbf{G_2}$ ($8^b_{G1}$ vs. $8^b_{G3}$) [95% CI $\mu_{(8^b_{G3})}-\mu_{(8^b_{G1})} = 6.39 \pm 6.57°$; *t*-test, $P = 0.053$).

While there were clear, positive transfer effects from isometric training to free motion, it is also clear that isometric training does not fully replace free motion training. Immediately after switching from isometric to free motion, subjects in the *transfer effects rVF* group (G1) moved comparably as straight as the *control* group (G3). However, after subsequent trials in free motion, subjects in the *transfer effects rVF* group had a slight increase in the directional errors: comparison $\mathbf{H_2}$ ($7^b_{G1}$ vs. $7^e_{G1}$) [95% CI $\mu_{(7^e_{G1}-7^b_{G1})} = -8.80 \pm 6.08°$; paired *t*-test, $P < 0.01$]. The increase in the directional errors *1*) was not observed in the *control* group (G3): comparison $\mathbf{I_2}$ ($7^b_{G3}$ vs. $7^e_{G3}$) [95% CI $\mu_{(7^e_{G3}-7^b_{G3})} = 3.01 \pm 5.01°$; paired *t*-test, $P = 0.20$) and *2*) led to a statistically significant difference between groups: comparison $\mathbf{J_2}$ ($7^e_{G1}$ vs. $7^e_{G3}$) [95% CI $\mu_{(7^e_{G3})} - \mu_{(7^e_{G1})} = 9.05 \pm 6.97°$; *t*-test, $P < 0.05$]. In addition, while the average number of lateral movement corrections in free motion with rVF before and after training increased for both G1 and G3: comparisons Fig. 8*A* (pre-rVF G1 vs. post-rVF G1: 95% CI $\tilde{x}_{(pre^{rVF}_{G1} - post^{rVF}_{G1})} = (0.33, 1.03)$; Wilcoxon signed-rank test, $P < 0.01$] and (pre-rVF G3 vs. post-rVF G3: 95% CI $\tilde{x}_{(pre^{rVF}_{G3} - post^{rVF}_{G3})} = (0.04, 0.35)$; Wilcoxon signed-rank test, $P < 0.05$], G1 exhibited more lateral movement corrections in free motion with rVF after training compared with G3: comparison Fig. 8*A* (post-rVF G1 vs. post-rVF G3) [95% CI $\tilde{x}(post^{rVF}_{G3}) - \tilde{x}_{(post^{rVF}_{G1})} = (-0.8, -0.2)$; Mann-Whitney test, $P < 0.01$]. The average number of lateral movement corrections in free motion with rNF after training was not statistically different between G2 and G3: comparison Fig. 8*B* (post-rNF G2 vs. post-rNF G3) [95% CI $\tilde{x}_{(post^{rNF}_{G3})} - \tilde{x}_{(post^{rNF}_{G1})} = (-0.03, 0.03)$; Mann-Whitney test, $P = 0.249$).

## DISCUSSION

This study provided early evidence supporting that training movement skills without moving is possible. Isometric training required subjects to apply coordinated forces on a handle as their arms were constrained to a static, i.e., isometric, position. A nonlinear dynamic simulation of horizontal arm reaching was used to make a graphic rendering of an avatar arm moving realistically in response to the measured interaction forces. The underlying assumptions of the simulated reaching dynamics approximated the association between muscle-generated forces and motion. The avatar arm was displayed on a horizontal display that blocked the view to their actual arm, encouraging subjects to believe the avatar's movements represented their own. With this setup, we observed a positive transfer of skills from an isometric to a free motion condition. Subjects were able to move straight in the presence of a disturbing force field after isometric training (*experiment 1*). We found that subjects were able to control isometric forces to make an avatar arm reach with relatively straight trajectories (as if moving in free motion). To discard possible confounding factors introduced by exposure to the actual dynamic environment during the measurement of the transfer effects in *experiment 1*, we performed a follow-up evaluation that tested the robustness and nature of this approach (*experiment 2*). Using pre- vs. postevaluations, without using intermittent trials, we evaluated whether participants were able to compensate for an actual force field in free motion (*experiment 2*, *transfer effects rVF* group). Furthermore, following isometric training, subjects exhibited curved movements when moving without the presence of the force field (null field), indicating aftereffects and hence a learning effect (*experiment 2*, *transfer effects rNF* group). Essentially, these experiments provided evidence that participants can learn to move straight in a deviating, velocity-dependent force field, without ever actually experiencing it. However, it is also clear that isometric training does not fully replace free motion training. While subjects were able to move relatively straight in the presence of a disturbing force field

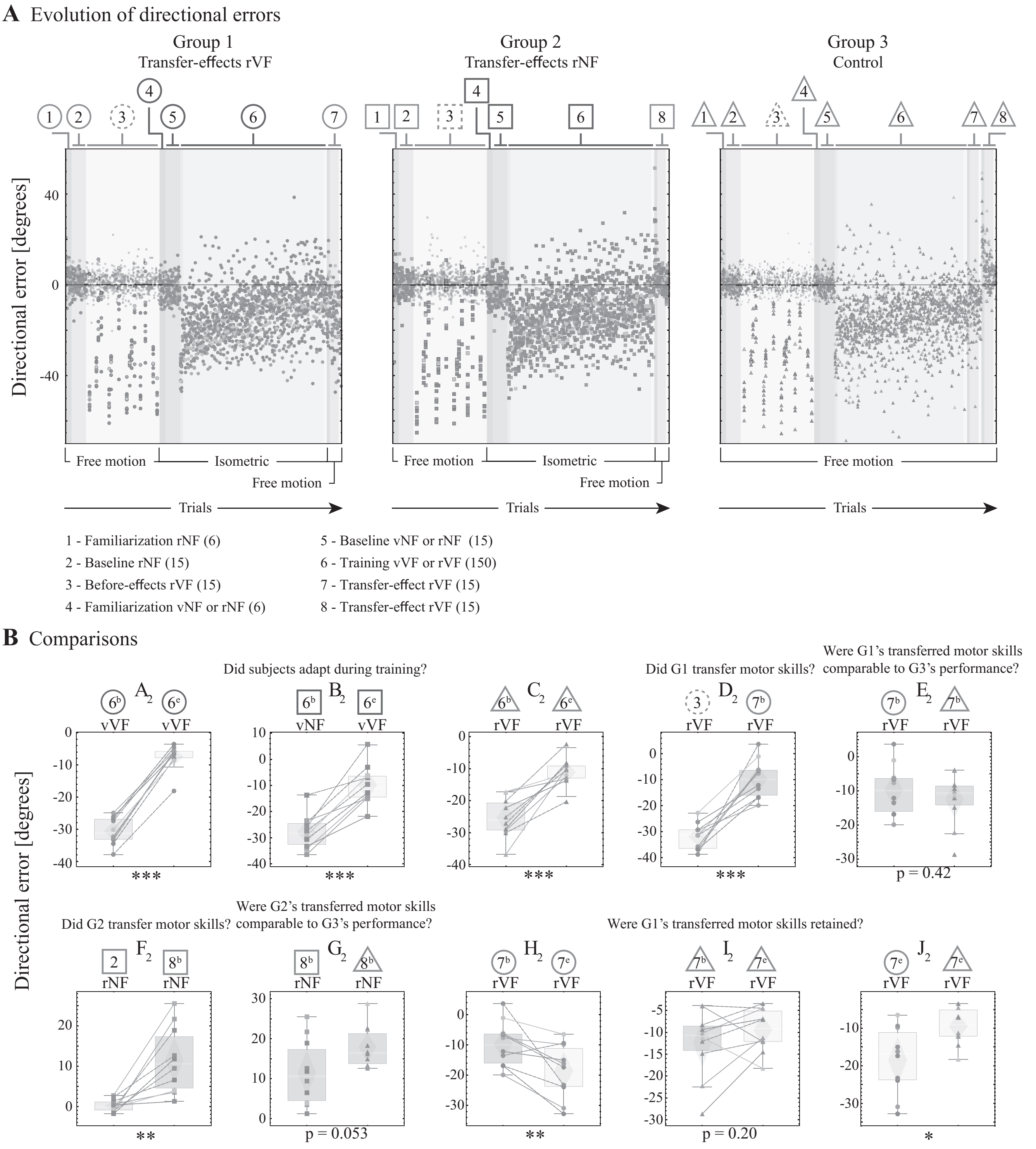


Fig. 7. *Top*: directional errors during the different experimental phases and groups of *experiment 2*. Note: For statistical comparisons, we denote with the superscripts b and e the beginning or end of a phase. For these subphases, we considered the first or last three (or less) nonoutlier trials within a window of six trials at the beginning or end of a phase.

after isometric training, we also found that these subjects tended to perform more lateral movement corrections than subjects who trained in free motion.

It is possible that a simpler proxy of the hand position, e.g., a cursor instead of an avatar, would have elicited the same results. However, in a recent paper (Farshchiansadegh et al. 2016) we found that, when physically interacting with a double pendulum (similar to a simplified arm), people move differently when they see a double pendulum or just a cursor. In general, it has been shown that perception of body motion is highly influenced by how an avatar is rendered (see e.g., Hodgins et al. 1998). Since we are interested in understanding

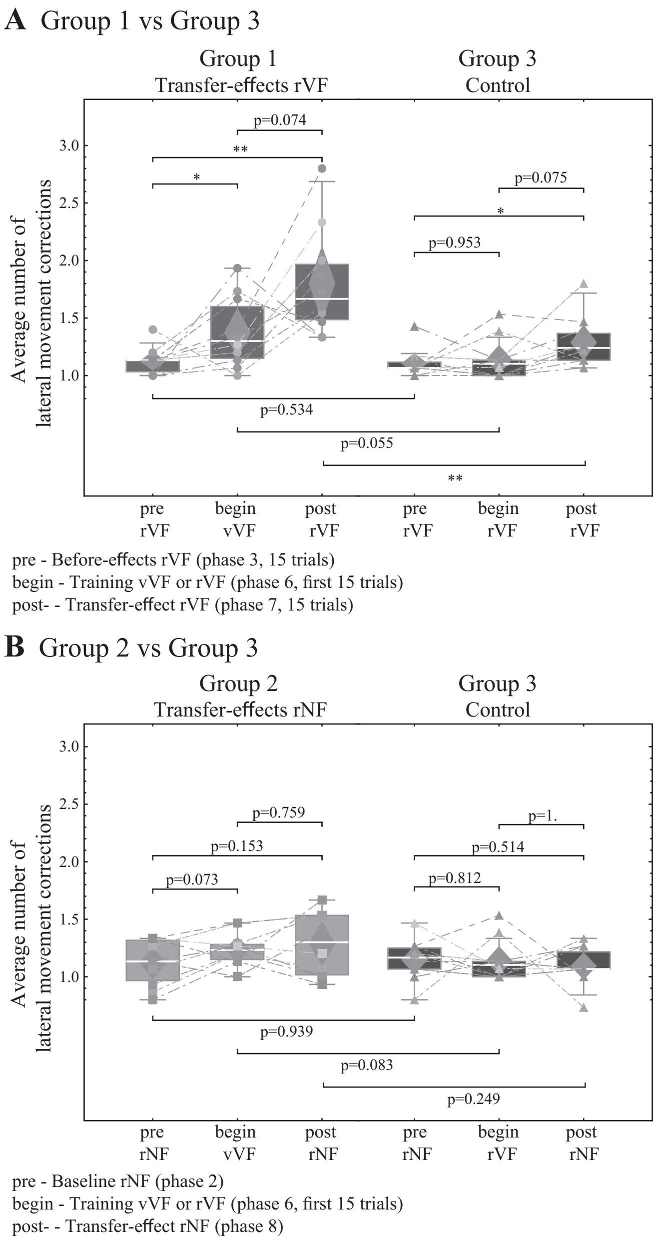


Fig. 8. Average number of movement corrections (*experiment 2*).

natural movements with (future) application in physical rehabilitation, we believe that results and conclusions obtained with the avatar choice (instead of a cursor) may be more representative and generalizable to actual movements in particular for neurologically affected individuals.

This study extends previous work in which information from a sensory modality (e.g., vision, proprioception) is distorted to shape motor adaptation. Our previous studies suggest that it is indeed possible to learn a force field along a reaching movement constrained to a "channel" joining the origin of the movement and the target. Such learning is achieved by presenting a subject with visual feedback corresponding to the force exerted on the channel during movement (Melendez-Calderon et al. 2009; Melendez-Calderon et al. 2011; Tommasino et al. 2014). While these works demonstrated that kinesthetic error can be replaced by equivalent visual error, tactile, and proprioceptive feedback of movement after learning was only slightly different between movements with or without the channel. Thus it may not be surprising that subjects in these previous studies could transfer the learned movement to a free movement condition. In contrast to our previous work in a channel, isometric training in this study involved sensory feedback from muscle spindle, cutaneous afferents, Golgi tendon organs, and other mechanoreceptors that were all different from the corresponding free motion condition. Therefore, it was unclear whether isometric training would transfer to the movement condition, or whether it would result in poorly performance due to a misrepresentation of the relationship between sensory signals and movement. Through the two complementary experiments of this study, the evidence appears to be that partial, yet substantial, transfer of motor skills is obtainable.

Considering the possible confusion that sensory discrepancies might bring to the CNS, our results support the idea of sensor-independent representation of movements. It is well known that visual distortions can stimulate motor adaptation and perception (Brewer et al. 2004; Ernst and Banks 2002; Flanagan and Rao 1995; Körding and Wolpert 2004; Robles-De-La-Torre and Hayward 2001; Sainburg et al. 2003; Srinivasan and LaMotte 1995) and influence the way dynamic environments are learned (Heuer and Hegele 2008; Liu et al. 2006; Todorov et al. 1997). Deceptive feedback can cause subjects to apply larger forces (Brewer et al. 2005) or can accelerate learning by amplifying error information (Patton et al. 2013; Patton et al. 2006; Wei et al. 2005a, 2005b). Isometric training allowed for the trainees to make relevant visual errors and use feedback to learn how to regulate motor commands during the activity. As Biocca et al. (2001) suggested, "limited haptic information can be compensated with appropriate synesthetic stimulation to other sensory modalities." Our results suggest that the discrepant proprioceptive information in isometric conditions was overridden by a visual synesthetic illusion and other forms of feedback, which encouraged sensorimotor adaptation that proved useful. These results also agree with the good motor performances of neuropathic subjects who are deprived of proprioceptive feedback (Ghez et al. 1995; Gordon et al. 1995; Sarlegna et al. 2010).

### *What Are the Possible Mechanisms That Enabled Subjects To Learn This Task?*

In a recent paper, Casadio et al. (2015) suggested that the CNS may combine two independent control modules, force and motion, to generate "compatible force/motion pairs" that allow the learning of arbitrary motions in contact with the environment. During isometric training in our experiment, we required subjects to learn to produce a specific contact force that translated into a specific motion of the avatar arm. Although there was not actual motion during this condition, it is possible that the CNS learned a compatible perceived force/motion pair that enable subjects to compensate for the actual environment in free motion. However, perception body motion is influenced by how information from multiple sensory modalities is combined and otherwise processed (Blanke et al. 2015; Dichgans and Brandt 1978; Graziano 1999; Kalckert and Ehrsson 2012; Lackner and DiZio 2000; Ostry et al. 2010). In our study, subjects were able to learn a compatible force/

motion pair based on deceptive proprioceptive information. A recent model of motor adaptation (Franklin et al. 2008; Tee et al. 2010) suggests that the CNS increases muscle activation based on muscle stretch or shortening in the previous movement. As muscle stretch or shortening resulting from errors was prevented in our paradigm, changes in muscle activation to compensate for the force field may have instead resulted from *1*) sensory reweighting or *2*) sensory realignment between vision and proprioception.

Sensory reweighting refers to the modification of the relative contribution of each sensory modality to an overall estimate of the arm position in space (Block and Bastian 2011; Ernst and Banks 2002; van Beers et al. 1999). The relative weight between visual and proprioceptive inputs depends on whether the fused output is used to determine the position of our own arm in space (Graziano 1999), to plan the direction of the movement (van Beers et al. 1999), or to plan motor command (Sober and Sabes 2005). It has been suggested that the CNS may combine the estimates from each sensory modality in a task-optimal manner and based on previous experience (Braun et al. 2009). But, in contrast to this view, some recent literature suggests a switched-input model, in which state estimates arising from vision and proprioception are maintained and used separately (Judkins and Scheidt 2014) with vision dominating proprioception. In contrast, sensory realignment refers to the modification on the estimate from one sensory modality to match the estimate of another sensory modality (Block and Bastian 2011; Ghahramani et al. 1997). The realignment mechanism is thought to be independent from reweighting, although they are both correlated such that the sensory modality with the lowest weight tends to realign the most (Block et al. 2013; Block and Bastian 2011).

In our experiment, we cannot elucidate which of these mechanisms were mainly responsible for the observed results. On one side, there is evidence of sensory reweighting (or a switch-input model) by the fact that subjects were able to transfer the acquired motor skills during isometric training to free motion with similar performance to subjects that only trained in the free motion condition (comparison $\mathbf{E_2}$ and $\mathbf{G_2}$); if the elicited mechanism would have been only sensory realignment, it is likely that the sudden mismatch between vision and proprioception after isometric training would have resulted in significantly different aftereffects. On the other side, we also found that subjects that trained in isometric exhibited more compensatory movements than those who trained in free motion (comparison post-rVF G1 vs. post-rVF G3) and that continuous exposure to free motion after isometric training resulted in additional adaptation (comparisons $\mathbf{E_1}$, $\mathbf{H_2}$, and $\mathbf{J_2}$). Such differences could be attributed to sensory realignment, although other factors such as incomplete adaptation or inaccuracies in the modeled dynamics of the avatar could also have played a role in the observed results.

### *What Are the Possible Neural Mechanisms That Adapted During Isometric Training?*

Different brain areas and neural mechanisms have been associated with reweighting and realignment. When monkeys had their arm moved with *1*) their arm uncovered (access to visual and proprioceptive information about arm position) or *2*) their arm covered (only proprioceptive information) or *3*) were shown an avatar of a monkey arm being moved (only visual information), the same group of neurons in the premotor cortex were activated (Graziano 1999). Graziano's study suggested that visual and proprioceptive inputs converge in the premotor cortex, encoding information about overall arm position. More recent primate studies found that Area 5 in the posterior parietal cortex is involved in the integration of visual and proprioceptive information to code arm position, which is connected to the premotor cortex (Buneo et al. 2002; Graziano et al. 2000). In humans, functional magnetic resonance imaging (fMRI) studies have also observed involvement of the parietal and premotor cortex in the integration of vision and proprioception related to the sense of limb ownership (Ehrsson et al. 2004). Using transcranial magnetic stimulation (TMS), Block et al. (2013) identified the angular gyrus as a potential brain area involved in proprioceptive alignment. Other regions, such as the anterior precuneus and the superior end of the parieto-occipital sulcus, are also involved in processing information from vision and proprioception, but their contribution depends on the sensory conditions during reaching (e.g., visual or nonvisual reaching) (Filimon et al. 2009). To investigate sensory reweighting, subsequent experiments can investigate whether there is increased or modified activity in the posterior parietal cortex in a similar paradigm to the one presented here but using fMRI-compatible technology (e.g., Gassert et al. 2006), or use TMS to produce "virtual lesions" (e.g., Block et al. 2013), to determine whether adaptation and transfer on our task is affected.

Furthermore, recent studies have highlighted the role of the cerebellum in the computation of sensory prediction errors and its relevance to movement adaptation and learning (Cullen and Brooks 2015; Krakauer and Mazzoni 2011; Wolpert et al. 1998). Since our results suggest a sensory-independent representation of errors, further experiments could investigate the extent of changes in the cerebellum caused by our paradigm as a proxy to further test our hypothesis. The sensitivity of proprioceptors and changes at the spinal circuitry level could have also adapted during our paradigm. During voluntary contractions, both alpha and gamma motor neurons are activated simultaneously (Hunt and Kuffler 1951) in a mechanism known as alpha-gamma coactivation. Static and dynamic sensitivity of muscles spindles (i.e., gain of Ia afferents) can be modulated by selective control of gamma motoneurons (Hulliger 1984; Prochazka 2010). It is possible that, during isometric training, muscle proprioceptive sensitivity was altered by gamma drive as a way to modify the relative weight of this modality to vision. Such changes in muscle spindle sensitivity would have direct consequences in the propriospinal pathway circuitry (Burke et al. 1992) and would require other spinal pathways such as Monosynaptic Ia excitation, Reciprocal Ia, Ib, and Renshaw inhibition (Pierrot-Deseilligny and Burke 2005) to adapt accordingly. Direct changes in these circuits, would have a big impact in the movement, as demonstrated by recent computational models of spinal circuitry, which have shown that adaptation to velocity-dependent force fields could be achieved by modifying the gains of spinal circuitries (Raphael et al. 2010). Further studies can incorporate electromyography recordings and postevaluation of reflexes to determine the extent to which such circuitry was altered.

Finally, neural representations of action observation or imagery are, to an extent, also engaged during movement execution (Jeannerod 2001; Macuga and Frey 2012). Such overlap may explain why people's performance on a particular task is influenced by pure observation of another person executing that task (Ikegami and Ganesh 2014; Kilner et al. 2003; Mattar and Gribble 2005). For instance, Mattar and Gribble (2005) had subjects watch a video of another person learning to perform reaching movements under the influence of a clockwise or a counterclockwise velocity-dependent force field; another group of subjects watched someone else performing reaching movements, but without adaptation. After the video demonstrations, observers performed reaching movements themselves under the influence of a clockwise field. Subjects who had watched another person adapting to the clockwise field performed better than those who watched similar movements but without adaptation. Subjects who watched another person adapting to the counterclockwise field performed the worst. Therefore, it is possible that the neural mechanisms engaged by the task similarity itself may have also contributed to the learning and transfer of motor skills in our paradigm.

### *Limitations of the Study*

This paper provides initial evidence that such an approach might have merit in training motor skills, but leaves some important open questions. It remains to be seen whether skills learned during isometric training conditions generalize to other unpracticed actions. However, speculating on this issue, we think that isometric training would not generalize to other parts of the workspace if the movement is far from arm configuration maintained during isometric training but would generalize to different target directions if the movement is close to the training conditions. Our rationale for this speculation is that isometric training is essentially a linearization of the controller around the posture maintained during the training. However, we think that more important than generalization to other part of the workspace is the transfer of skills from isometric to a free motion condition, which we present in this study. If one wants to train on a different workspace, one could simply change the initial arm configuration during different training sessions.

The work from Hwang et al. on adaptation to acceleration-dependent force fields (Hwang and Shadmehr 2005; Hwang et al. 2006) suggested that the internal representation of limb state may be driven by proprioceptive sensors, which encode position, velocity, and acceleration in a combined way. Therefore, it is yet to be tested whether adaptation to acceleration-dependent fields (e.g., gravity-loaded movements with objects), driven purely by vision, allows for similar encoding that would facilitate the transfer of motor skills to real scenarios.

It is also unclear whether actions requiring more degrees of freedom are possible to train isometrically. There is some evidence that the perception of movements differs for different movement directions (Wolpert et al. 1994) and that movements are adapted based on the perceived space (Flanagan and Rao 1995). Therefore, it is possible that multidimensional movements are harder to learn, just due to perceptual differences on the different movement directions caused by the display of visual information in the virtual environment. However, if isometric training does not generalize to multidimensional movements, partially constrained training (e.g., Melendez-Calderon et al. 2011) could also be a possibility, such as training three-dimensional movements with a simpler two- or one-dimensional device.

Finally, we chose the task of adapting to a velocity-dependent force field because such a force field does not alter the stability of the system and its compensation does not require increased muscle cocontraction. However, humans typically respond to any new, uncertain environment by cocontraction, which may subside during adaptation to the new environment (Franklin et al. 2003). Moreover, it is known that visual disturbances can induce changes muscle activation (Franklin and Wolpert 2008) and that muscle activation levels may differ significantly, even if the task requires subjects to maintain similar joint angles and torques (Buchanan and Lloyd 1995). Therefore, a limitation of our study is the lack of electromyography (EMG) recordings to compare differences between isometric and free motion training. In addition, real-time EMG measurements are required to investigate this approach in unstable or noisy force fields, since the avatar arm needs to adjust its mechanical impedance based on muscle cocontraction.

### *Applications of Isometric Training*

This study provides evidence for the concept of limited sensory training environments, where the user can later transfer skills and knowledge to real-world application. Such virtual environments allow for reduced, controlled, and less expensive environments; therefore, a potentially prominent target application area of this approach includes neurorehabilitation of movement disorders. Our premise is that by exploiting interactions between conflicting sensory stimuli, simple devices could foster learning of complex dynamics without the need of an apparatus with complicated mechanical structures such as multi-DOF robotic devices. Such an approach may enable home rehabilitation systems using solely a force sensor with an interactive display. Such motion-free training approaches may also be beneficial for patients that have spasms caused by moving, e.g., dystonia.

In any case, the isometric training paradigm presented here provides a new paradigm for probing how the nervous system uses sensory information to learn and control movements. It allows the exploration of the relative role of reweighting and recalibration of sensory modalities and the implication of such processes in the acquisition of motor skills. Our assertion is that, once this process is fully understood and modeled, it can target a variety of application areas.

## APPENDIX

### *Directional Error*

To define "directional error," let us define the following concepts:

- Origin-target line: line connecting the center of the origin and the center of the target (origin-target line)
- Ideal aiming line: line joining the cursor position at movement onset and the center of the target
- First speed peak tangent line: line tangent to the cursor position at the first speed peak that is at least 25% of the maximum speed and after 50 ms of movement onset
- First speed peak angle: angle between ideal aiming line and first speed peak tangent line
- First velocity peak tangent line: line tangent to the cursor position at the first absolute velocity peak in either parallel or perpendic-

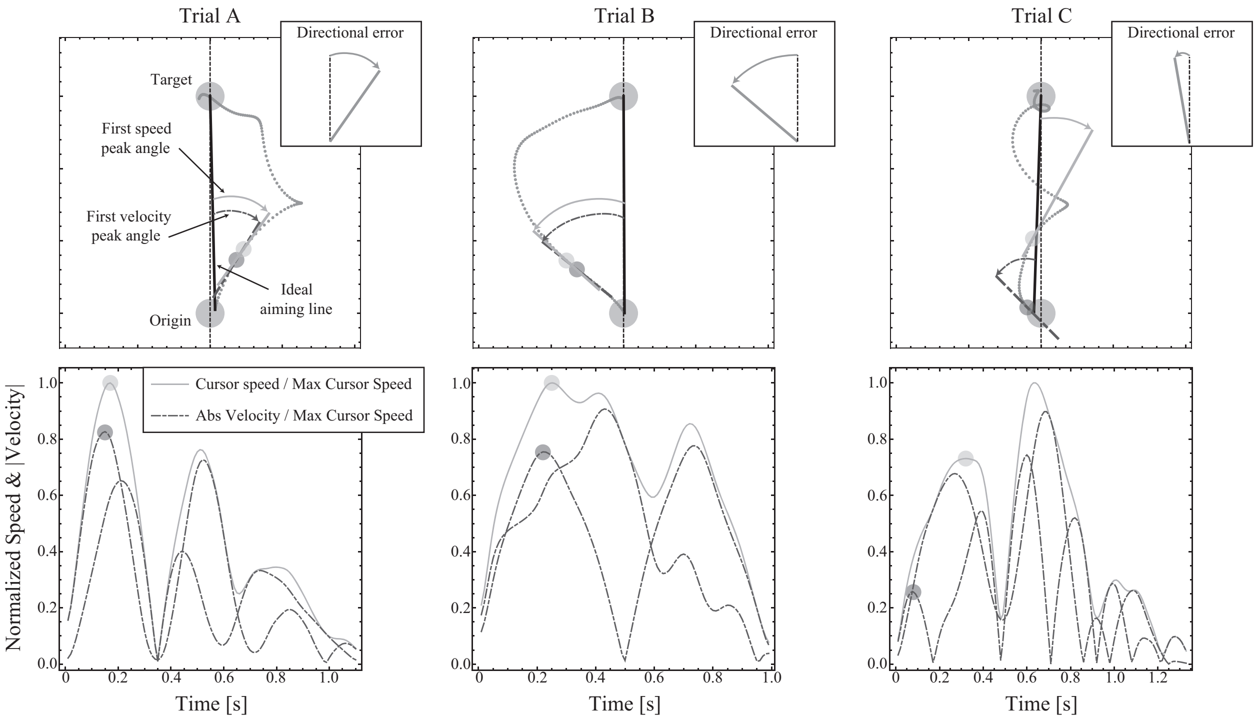


Fig. 9. Illustration of the directional error concept for different movements (*trials A–C*). Directional error was defined as the average between first speed peak angle and first velocity peak angle. Note how, in the case of *trial C*, this average is a fairer representation of the movement's lateral deviation; if one would consider the first speed peak angle only, *trial C* would be similar to *trial B*; if one would consider the first velocity peak angle only, *trial C* would be similar to *trial A*.

ular direction to the origin-target line that is at least 25% of the maximum speed and after 50 ms of movement onset

- First velocity peak angle: angle between ideal aiming line and first velocity peak tangent line

Directional error was defined as the average between first speed peak angle and first velocity peak angle. In contrast to computing directional error by only looking at the first speed peak angle, this averaging method is more effective at representing the lateral deviation of a movement as illustrated in Fig. 9.

## *Dynamics of the Avatar Arm*

During the isometric condition, forces that subjects applied against the physical brake were used to move a realistic rendering of an arm (avatar arm). Human arm dynamics presented in (Melendez-Calderon et al. 2011) were adapted to this paper's experimental paradigm. As in Burdet et al. 2006 and Tee et al. 2004, we assumed that the central nervous system controls the arm to compensate for its dynamics, muscle viscoelasticity and reflexes produce a restoring force that can be modeled as feedback. The dynamics of the avatar arm interacting with the environment were thus modeled as

$$H(q)\ddot{q} + C(q,\dot{q})\dot{q} = J(q)^T(F_{VF} + F_{Handle} - F_{Robot}) + \tau_{FB} \quad (3)$$

$F_{VF}$ corresponds to the force of the dynamic environment (as in *Eq. 1*), $F_{Handle}$ to the force applied by the subject against the robot when it is clamped, and $F_{Robot}$ to the modeled dynamics of the robot.

$H(q)$ is the arm inertia matrix and is defined as

$$\begin{aligned} H(q) &= \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \\ a_{11} &= J_1 + J_2 + m_1 l_{m1}^2 + m_2[l_1^2 + l_{m2}^2 + 2 l_1 l_{m2} Cos(q_2)] \\ a_{12} &= a_{21} = J_2 + m_2[l_{m2}^2 + l_1 l_{m2} Cos(q_2)] \\ a_{22} &= J_2 + m_2 l_{m2}^2 \end{aligned} \quad (4)$$

$q_1$ and $q_2$ denote the avatar arm's shoulder and elbow joint angles (rad), respectively, and are obtained from the inverse kinematic transformation of the avatar arm's hand center position. $l_1$ and $l_2$ denote the segment lengths of the subject's upper arm and forearm and hand (m), measured at the beginning of the experiment. $l_{m1}$ and $l_{m2}$ denote the upper arm and forearm and hand center of mass from proximal joint (in m), $m_1$ and $m_2$ the upper arm and forearm and hand masses (kg), and $J_1$ and $J_2$ the upper arm and forearm and hand mass moment of inertia (kg m$^2$). These subject-specific parameters were estimated by measuring the body mass, $m_{subject}$, and limb segments, $l_1$ and $l_2$, of each subject at the beginning of the experiment and using the anthropometrical tables from Winter (2004) as follows:

$$\begin{aligned} m_1 &= 0.028 m_{subject} \\ m_2 &= 0.022 m_{subject} \\ l_{m1} &= 0.436 l_1 \\ l_{m2} &= 0.682 l_2 \\ J_1 &= (0.542 l_1)^2 m_1 \\ J_2 &= (0.827 l_2)^2 m_2 \end{aligned} \quad (5)$$

$C(q,\dot{q})\dot{q}$ is the term corresponding to Coriolis and centripetal forces and is defined as

$$C(q,\dot{q})\dot{q} = \begin{bmatrix} -m_2 l_1 l_{m2} \dot{q}_2(2\dot{q}_1 + \dot{q}_2)\sin(q_2) \\ m_2 l_1 l_{m2} \dot{q}_1{}^2 \sin(q_2) \end{bmatrix} \quad (6)$$

The Jacobian matrix transforming end point force into joint torque is given by

$$J(q) = \begin{bmatrix} -l_1\sin(q_1) - l_2\sin(q_1 + q_2) & -l_2\sin(q_1 + q_2) \\ l_1\cos(q_1) + l_2\cos(q_1 + q_2) & l_2\cos(q_1 + q_2) \end{bmatrix} \quad (7)$$

The feedback torque, $\tau_{FB}$, produces a restoring force toward a planned trajectory $q_d$. $\tau_{FB}$ is proportional to the end point speed by a factor lambda, λ (*Eq. 8*), to avoid the avatar arm to move by itself.

Heuristically, this term helped to stabilize the avatar arm's movement when it moved relatively "fast" and it was difficult to control the avatar's motion based on purely visual feedback. Note that a high λ would make the avatar arm move by itself without any effort from the subject, whereas a low λ would let the subject stabilize the movement based on visual feedback corrections.

$$\tau_{FB} = \lambda\left[K\left(q_d - q\right) + D(\dot{q}_d - \dot{q})\right]$$
$$\lambda = \begin{cases} Speed/threshold, & Speed < threshold \\ 1.0, & \left|Speed \geq threshold\right. \end{cases} \tag{8}$$
$$threshold = 0.8\ (m/s)$$

$K$ (N m/rad) is the mean torque-dependent joint stiffness from the subjects measured by Gomi and Osu (1998), which is a function of the feedforward torque $\tau_{FF}$, defined as

$$K(\tau_{FF}) = \begin{pmatrix} 10.8 + 3.18\left|\tau_{FF1}\right| & 2.83 + 2.15\left|\tau_{FF2}\right| \\ 2.51 + 2.34\left|\tau_{FF2}\right| & 8.67 + 6.18\left|\tau_{FF2}\right| \end{pmatrix} \tag{9}$$

The feedforward torque $\tau_{FF}$ was estimated by inverse dynamics based on the kinematics of the planned trajectory $q_d$. The term $D$ (N m s/rad)corresponds to the viscosity in joint space, which is nonlinearly related to joint stiffness and depends on velocity (Tee et al. 2004), defined as

$$D = (0.42/\sqrt{\dot{q}^T\dot{q} + 1})K \tag{10}$$

The planned trajectory $q_d$ was computed from the inverse kinematics of a minimum-jerk trajectory in end point space, $X_d$.

$$\begin{aligned} x_{d1} &= 0 \\ x_{d2} &= \frac{\begin{pmatrix} 12 * movLength - 12 * y_0 - 6 * movDuration * \\ \dot{y}_0 - movTime^2 * \ddot{y}_0 \end{pmatrix} t^5}{2 * movDuration^5} \\ &\quad - \frac{\begin{pmatrix} 30 * movLength - 30 * y_0 - 16 * movDuration * \\ \dot{y}_0 - 3 * movDuration^2 * \ddot{y}_0 \end{pmatrix} t^4}{2 * movDuration^4} \\ &\quad + \frac{\begin{pmatrix} 20 * movLength - 20 * y_0 - 12 * movDuration * \\ \dot{y}_0 - 3 * movDuration^2 * \ddot{y}_0 \end{pmatrix} t^3}{2 * movDuration^3} \\ &\quad + \frac{\ddot{y}_0 t^2}{2} + \dot{y}_0 t + y_0 \\ X_q &= R_\theta \cdot \begin{pmatrix} x_{d1} \\ x_{d2} \end{pmatrix} \end{aligned} \tag{11}$$

where *movLength* is the requested movement length (i.e., the target distance); *movDuration* is the requested movement duration; $y_0$, $\dot{y}_0$, and $\ddot{y}_0$ correspond to the instantaneous avatar hand's position, velocity, and acceleration along the axis that connects the origin with a particular target at movement onset; and $R_\theta$ is a rotation matrix that rotates the trajectory $x_{d2}$ in the direction of a particular target.

Force produced by the robot dynamics, $F_{Robot}$ was approximated by end point mass of 0.75 kg with a viscous friction of 15 N s/m.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

A.M.-C. conceived and designed research; A.M.-C., M.T., and M.F.B. performed experiments; A.M.-C. and M.T. analyzed data; A.M.-C., M.T., M.F.B., E.B., and J.L.P. interpreted results of experiments; A.M.-C. prepared Figures; A.M.-C., M.T., M.F.B., and J.L.P. drafted manuscript; A.M.-C., M.T., M.F.B., E.B., and J.L.P. edited and revised manuscript; A.M.-C., M.T., M.F.B., E.B., and J.L.P. approved final version of manuscript.

## References

**Berniker M, Kording K.** Estimating the sources of motor errors for adaptation and generalization. *Nat Neurosci* 11: 1454–1461, 2008. doi:10.1038/nn.2229.

**Biocca F, Kim J, Choi Y.** Visual touch in virtual environments: an exploratory study of presence, multimodal interfaces, and cross-modal sensory illusions. *Presence* 10: 247–265, 2001.

**Blanke O, Slater M, Serino A.** Behavioral, neural, and computational principles of bodily self-consciousness. *Neuron* 88: 145–166, 2015. doi:10.1016/j.neuron.2015.09.029.

**Block H, Bastian A, Celnik P.** Virtual lesion of angular gyrus disrupts the relationship between visuoproprioceptive weighting and realignment. *J Cogn Neurosci* 25: 636–648, 2013. doi:10.1162/jocn_a_00340.

**Block HJ, Bastian AJ.** Sensory weighting and realignment: independent compensatory processes. *J Neurophysiol* 106: 59–70, 2011. doi:10.1152/jn.00641.2010.

**Brashers-Krug T, Shadmehr R, Bizzi E.** Consolidation in human motor memory. *Nature* 382: 252–255, 1996. doi:10.1038/382252a0.

**Braun DA, Aertsen A, Wolpert DM, Mehring C.** Learning optimal adaptation strategies in unpredictable motor tasks. *J Neurosci* 29: 6472–6478, 2009. doi:10.1523/JNEUROSCI.3075-08.2009.

**Brewer BR, Fagan M, Klatzky RL, Matsuoka Y.** Perceptual limits for a robotic rehabilitation environment using visual feedback distortion. *IEEE Trans Neural Syst Rehabil Eng* 13: 1–11, 2005. doi:10.1109/TNSRE.2005.843443.

**Brewer BR, Klatzky R, Matsuoka Y.** Effects of visual feedback distortion for the elderly and the motor-impaired in a robotic rehabilitation environment. IEEE International Conference on Robotics and Automation (ICRA), New Orleans, LA, 2004.

**Buchanan TS, Lloyd DG.** Muscle activity is different for humans performing static tasks which require force control and position control. *Neurosci Lett* 194: 61–64, 1995. doi:10.1016/0304-3940(95)11727-E.

**Buneo CA, Jarvis MR, Batista AP, Andersen RA.** Direct visuomotor transformations for reaching. *Nature* 416: 632–636, 2002. doi:10.1038/416632a.

**Burdet E, Tee KP, Mareels I, Milner TE, Chew CM, Franklin DW, Osu R, Kawato M.** Stability and motor adaptation in human arm movements. *Biol Cybern* 94: 20–32, 2006. doi:10.1007/s00422-005-0025-9.

**Burke D, Gracies JM, Mazevet D, Meunier S, Pierrot-Deseilligny E.** Convergence of descending and various peripheral inputs onto common propriospinal-like neurones in man. *J Physiol* 449: 655–671, 1992. doi:10.1113/jphysiol.1992.sp019107.

**Casadio M, Pressman A, Mussa-Ivaldi FA.** Learning to push and learning to move: the adaptive control of contact forces. *Front Comput Neurosci* 9: 118, 2015. doi:10.3389/fncom.2015.00118.

**Casadio M, Sanguineti V, Solaro C, Morasso PG.** A haptic robot reveals the adaptation capability of individuals with multiple sclerosis. *Int J Robot Res* 26: 1225–1233, 2007. doi:10.1177/0278364907084981.

**Conditt MA, Gandolfo F, Mussa-Ivaldi FA.** The motor system does not learn the dynamics of the arm by rote memorization of past experience. *J Neurophysiol* 78: 554–560, 1997.

**Cullen KE, Brooks JX.** Neural correlates of sensory prediction errors in monkeys: evidence for internal models of voluntary self-motion in the cerebellum. *Cerebellum* 14: 31–34, 2015. doi:10.1007/s12311-014-0608-x.

**Dichgans J, Brandt T.** Visual-vestibular interaction: effects on self-motion perception and postural control. In *Perception*, edited by Held R, Leibowitz

HW, Teuber H-L. Berlin: Springer, 1978, p. 755–804. doi:10.1007/978-3-642-46354-9_25.

**Dominjon L, Lecuyer A, Burkhardt JM, Richard P, Richir S.** Influence of control/display ratio on the perception of mass of manipulated objects in virtual environments. In: *Virtual Reality, 2005 Proceedings VR 2005 IEEE*, 2005, p. 19–25.

**Donchin O, Francis JT, Shadmehr R.** Quantifying generalization from trial-by-trial behavior of adaptive systems that learn with basis functions: theory and experiments in human motor control. *J Neurosci* 23: 9032–9045, 2003.

**Ehrsson HH, Spence C, Passingham RE.** That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305: 875–877, 2004. doi:10.1126/science.1097011.

**Ernst MO, Banks MS.** Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415: 429–433, 2002. doi:10.1038/415429a.

**Farshchiansadegh A, Melendez-Calderon A, Ranganathan R, Murphey TD, Mussa-Ivaldi FA.** Sensory agreement guides kinetic energy optimization of arm movements during object manipulation. *PLOS Comput Biol* 12: e1004861, 2016. doi:10.1371/journal.pcbi.1004861.

**Filimon F, Nelson JD, Huang R-S, Sereno MI.** Multiple parietal reach regions in humans: cortical representations for visual and proprioceptive feedback during on-line reaching. *J Neurosci* 29: 2961–2971, 2009. doi:10.1523/JNEUROSCI.3211-08.2009.

**Flanagan JR, Nakano E, Imamizu H, Osu R, Yoshioka T, Kawato M.** Composition and decomposition of internal models in motor learning under altered kinematic and dynamic environments. *J Neurosci* 19: RC34, 1999.

**Flanagan JR, Rao AK.** Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. *J Neurophysiol* 74: 2174–2178, 1995.

**Franklin DW, Burdet E, Tee KP, Osu R, Chew CM, Milner TE, Kawato M.** CNS learns stable, accurate, and efficient movements using a simple algorithm. *J Neurosci* 28: 11165–11173, 2008. doi:10.1523/JNEUROSCI.3099-08.2008.

**Franklin DW, Osu R, Burdet E, Kawato M, Milner TE.** Adaptation to stable and unstable dynamics achieved by combined impedance control and inverse dynamics model. *J Neurophysiol* 90: 3270–3282, 2003. doi:10.1152/jn.01112.2002.

**Franklin DW, So U, Burdet E, Kawato M.** Visual feedback is not necessary for the learning of novel dynamics. *PLoS One* 2: e1336, 2007. doi:10.1371/journal.pone.0001336.

**Franklin DW, Wolpert DM.** Specificity of reflex adaptation for task-relevant variability. *J Neurosci* 28: 14165–14175, 2008. doi:10.1523/JNEUROSCI.4406-08.2008.

**Gassert R, Dovat L, Lambercy O, Ruffieux Y, Chapuis D, Ganesh G, Burdet E, Bleuler H.** A 2-DOF fMRI compatible haptic interface to investigate the neural control of arm movements. *2006 IEEE International Conference on Robotics and Automation (ICRA)*, 3825–3831, 2006.

**Ghahramani Z, Wolpert DM, Jordan MI.** Computational models of sensorimotor integration. In: *Self-Organization, Computational Maps, and Motor Control*, edited by Morasso P, Sanguineti V. Amsterdam: North-Holland, 1997, p. 117–147. Advances in Psychology

**Ghez C, Gordon J, Ghilardi MF.** Impairments of reaching movements in patients without proprioception. II. Effects of visual information on accuracy. *J Neurophysiol* 73: 361–372, 1995.

**Gomi H, Osu R.** Task-dependent viscoelasticity of human multijoint arm and its spatial characteristics for interaction with environments. *J Neurosci* 18: 8965–8978, 1998.

**Gordon J, Ghilardi MF, Ghez C.** Impairments of reaching movements in patients without proprioception. I. Spatial errors. *J Neurophysiol* 73: 347–360, 1995.

**Graziano MSA.** Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc Natl Acad Sci USA* 96: 10418–10421, 1999. doi:10.1073/pnas.96.18.10418.

**Graziano MSA, Cooke DF, Taylor CSR.** Coding the location of the arm by sight. *Science* 290: 1782–1786, 2000. doi:10.1126/science.290.5497.1782.

**Herzfeld DJ, Vaswani PA, Marko MK, Shadmehr R.** A memory of errors in sensorimotor learning. *Science* 345: 1349–1353, 2014. doi:10.1126/science.1253138.

**Heuer H, Hegele M.** Constraints on visuo-motor adaptation depend on the type of visual feedback during practice. *Exp Brain Res* 185: 101–110, 2008. doi:10.1007/s00221-007-1135-5.

**Hodgins JK, O'Brien JF, Tumblin J.** Perception of human motion with different geometric models. *IEEE Trans Vis Comput Graph* 4: 307–316, 1998. doi:10.1109/2945.765325.

**Hulliger M.** The mammalian muscle spindle and its central control. *Rev Physiol Biochem Pharmacol* 101: 1–110, 1984. doi:10.1007/BFb0027694.

**Hunt CC, Kuffler SW.** Stretch receptor discharges during muscle contraction. *J Physiol* 113: 298–315, 1951.

**Hwang EJ, Shadmehr R.** Internal models of limb dynamics and the encoding of limb state. *J Neural Eng* 2: S266–S278, 2005. doi:10.1088/1741-2560/2/3/S09.

**Hwang EJ, Smith MA, Shadmehr R.** Adaptation and generalization in acceleration-dependent force fields. *Exp Brain Res* 169: 496–506, 2006. doi:10.1007/s00221-005-0163-2.

**Ikegami T, Ganesh G.** Watching novice action degrades expert motor performance: causation between action production and outcome prediction of observed actions by humans. *Sci Rep* 4: 6989, 2014. doi:10.1038/srep06989.

**Jeannerod M.** Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage* 14: S103–S109, 2001. doi:10.1006/nimg.2001.0832.

**Judkins T, Scheidt RA.** Visuo-proprioceptive interactions during adaptation of the human reach. *J Neurophysiol* 111: 868–887, 2014. doi:10.1152/jn.00314.2012.

**Kalckert A, Ehrsson HH.** Moving a rubber hand that feels like your own: a dissociation of ownership and agency. *Front Hum Neurosci* 6: 40, 2012. doi:10.3389/fnhum.2012.00040.

**Kilner JM, Paulignan Y, Blakemore SJ.** An interference effect of observed biological movement on action. *Curr Biol* 13: 522–525, 2003. doi:10.1016/S0960-9822(03)00165-9.

**Körding KP, Wolpert DM.** Bayesian integration in sensorimotor learning. *Nature* 427: 244–247, 2004. doi:10.1038/nature02169.

**Krakauer JW, Mazzoni P.** Human sensorimotor learning: adaptation, skill, and beyond. *Curr Opin Neurobiol* 21: 636–644, 2011. doi:10.1016/j.conb.2011.06.012.

**Lackner JR, DiZio PA.** Aspects of body self-calibration. *Trends Cogn Sci* 4: 279–288, 2000. doi:10.1016/S1364-6613(00)01493-5.

**Lecuyer A.** Simulating haptic feedback using vision: a survey of research and applications of pseudo-haptic feedback. *Presence* 18: 39–53, 2009.

**Lecuyer A, Congedo M, Gentaz E, Joly O, Coquillart S.** Influence of visual feedback on passive tactile perception of speed and spacing of rotating gratings. In: *Haptics: Generating and Perceiving Tangible Sensations*, edited by Kappers A, van Erp J, Bergmann Tiest W, van der Helm F. Berlin: Springer, 2010, p. 73–78.

**Liu J, Cramer SC, Reinkensmeyer DJ.** Learning to perform a new movement with robotic assistance: comparison of haptic guidance and visual demonstration. *J Neuroeng Rehabil* 3: 20, 2006. doi:10.1186/1743-0003-3-20.

**Macuga KL, Frey SH.** Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage* 59: 2798–2807, 2012. doi:10.1016/j.neuroimage.2011.09.083.

**Mah CD, Mussa-Ivaldi FA.** Generalization of object manipulation skills learned without limb motion. *J Neurosci* 23: 4821–4825, 2003.

**Mattar AAG, Gribble PL.** Motor learning by observing. *Neuron* 46: 153–160, 2005. doi:10.1016/j.neuron.2005.02.009.

**Melendez-Calderon A, Fisher M, Tan M, Burdet E, Patton JL.** Acquisition of motor skills in isometric conditions through synesthetic illusions of movement. In: *World Haptics Conference (WHC), 2015 IEEE*, 2015, p. 428–433.

**Melendez-Calderon A, Masia L, Casadio M, Burdet E.** Force field compensation can be learned without proprioceptive error. In: *IFMBE Proceedings, World Congress on Medical Physics and Biomedical Engineering*. Munich, Germany: Springer, 2009, p. 381–383.

**Melendez-Calderon A, Masia L, Gassert R, Sandini G, Burdet E.** Force field adaptation can be learned using vision in the absence of proprioceptive error. *IEEE Trans Neural Syst Rehabil Eng* 19: 298–306, 2011. doi:10.1109/TNSRE.2011.2125990.

**Ostry DJ, Darainy M, Mattar AA, Wong J, Gribble PL.** Somatosensory plasticity and motor learning. *J Neurosci* 30: 5384–5393, 2010. doi:10.1523/JNEUROSCI.4571-09.2010.

**Patton JL, Wei Y, Scharver C, Kenyon RV, Scheidt R.** Motivating rehabilitation by distorting reality. In: *BioRob 2006: The first IEEE/RAS-EMBS International Conference on Biomedical Robotics and Biomechatronics*, Pisa, Italy, 2006.

**Patton JL, Wei YJ, Bajaj P, Scheidt RA.** Visuomotor learning enhanced by augmenting instantaneous trajectory error feedback during reaching. *PLoS One* 8: e46466, 2013. doi:10.1371/journal.pone.0046466.

**Pierrot-Deseilligny E, Burke D.** *The Circuitry of the Human Spinal Cord: Its Role in Motor Control and Movement Disorders*. Cambridge, UK: Cambridge University Press, 2005. doi:10.1017/CBO9780511545047.

**Prochazka A.** Proprioceptive feedback and movement regulation. *Compr Physiol*, 2011. doi:10.1002/cphy.cp120103.

**Raphael G, Tsianos GA, Loeb GE.** Spinal-like regulator facilitates control of a two-degree-of-freedom wrist. *J Neurosci* 30: 9431–9444, 2010. doi:10.1523/JNEUROSCI.5537-09.2010.

**Robles-De-La-Torre G, Hayward V.** Force can overcome object geometry in the perception of shape through active touch. *Nature* 412: 445–448, 2001. doi:10.1038/35086588.

**Rotella MF, Nisky I, Koehler M, Rinderknecht MD, Bastian AJ, Okamura AM.** Learning and generalization in an isometric visuomotor task. *J Neurophysiol* 113: 1873–1884, 2015. doi:10.1152/jn.00255.2014.

**Sainburg RL, Lateiner JE, Latash ML, Bagesteiro LB.** Effects of altering initial position on movement direction and extent. *J Neurophysiol* 89: 401–415, 2003. doi:10.1152/jn.00243.2002.

**Sarlegna FR, Malfait N, Bringoux L, Bourdin C, Vercher JL.** Force-field adaptation without proprioception: can vision be used to model limb dynamics? *Neuropsychologia* 48: 60–67, 2010. doi:10.1016/j.neuropsychologia.2009.08.011.

**Saville DJ.** Multiple comparison procedures: the practical solution. *Am Stat* 44: 174–180, 1990.

**Schabowsky CN, Hidler JM, Lum PS.** Greater reliance on impedance control in the nondominant arm compared with the dominant arm when adapting to a novel dynamic environment. *Exp Brain Res* 182: 567–577, 2007. doi:10.1007/s00221-007-1017-x.

**Scheidt RA, Conditt MA, Secco EL, Mussa-Ivaldi FA.** Interaction of visual and proprioceptive feedback during adaptation of human reaching movements. *J Neurophysiol* 93: 3200–3213, 2005. doi:10.1152/jn.00947.2004.

**Shadmehr R, Mussa-Ivaldi FA.** Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14: 3208–3224, 1994.

**Smith MA, Shadmehr R.** Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J Neurophysiol* 93: 2809–2821, 2005. doi:10.1152/jn.00943.2004.

**Sober SJ, Sabes PN.** Flexible strategies for sensory integration during motor planning. *Nat Neurosci* 8: 490–497, 2005.

**Srinivasan MA, LaMotte RH.** Tactual discrimination of softness. *J Neurophysiol* 73: 88–101, 1995.

**Takiyama K, Hirashima M, Nozaki D.** Prospective errors determine motor learning. *Nat Commun* 6: 5925, 2015. doi:10.1038/ncomms6925.

**Tee KP, Burdet E, Chew CM, Milner TE.** A model of force and impedance in human arm movements. *Biol Cybern* 90: 368–375, 2004. doi:10.1007/s00422-004-0484-4.

**Tee KP, Franklin DW, Kawato M, Milner TE, Burdet E.** Concurrent adaptation of force and impedance in the redundant muscle system. *Biol Cybern* 102: 31–44, 2010. doi:10.1007/s00422-009-0348-z.

**Thoroughman KA, Shadmehr R.** Learning of action through adaptive combination of motor primitives. *Nature* 407: 742–747, 2000. doi:10.1038/35037588.

**Todorov E, Shadmehr R, Bizzi E.** Augmented feedback presented in a virtual environment accelerates learning of a difficult motor task. *J Mot Behav* 29: 147–158, 1997. doi:10.1080/00222899709600829.

**Tommasino P, Melendez-Calderon A, Burdet E, Campolo D.** Motor adaptation with passive machines: a first study on the effect of real and virtual stiffness. *Comput Methods Programs Biomed* 116: 145–155, 2014. doi:10.1016/j.cmpb.2013.12.019.

**van Beers RJ, Sittig AC, Gon JJ.** Integration of proprioceptive and visual position-information: an experimentally supported model. *J Neurophysiol* 81: 1355–1364, 1999.

**Wei Y, Bajaj P, Scheidt R, Patton J.** Visual error augmentation for enhancing motor learning and rehabilitative relearning. In: *ICORR 2005 9th International Conference on Rehabilitation Robotics, 2005*. 2005a, p. 505–510.

**Wei Y, Bajaj P, Scheidt RA, Patton JL.** A real-time haptic/graphic demonstration of how error augmentation can enhance learning. In: *IEEE International Conference on Robotics and Automation (ICRA)*. Barcelona: 2005b.

**Winter DA.** *Biomechanics and Motor Control of Human Movement* (3rd ed.). Hoboken, NJ: Wiley, 2004.

**Wolpert DM, Ghahramani Z, Jordan MI.** Perceptual distortion contributes to the curvature of human reaching movements. *Exp Brain Res* 98: 153–156, 1994. doi:10.1007/BF00229120.

**Wolpert DM, Miall RC, Kawato M.** Internal models in the cerebellum. *Trends Cogn Sci* 2: 338–347, 1998. doi:10.1016/S1364-6613(98)01221-2.