Behavioral/Cognitive

Eliminating Direction Specificity in Visuomotor Learning

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The generalization of learning offers a unique window for investigating the nature of motor learning. Error-based motor lea
reportedly cannot generalize to distant directions because the aftereffects are direction specific. This direction specificity is o
garded as evidence that motor adaptation is model-based learning, and is constrained by neuronal tuning characteristics in the
motor cortices and the cerebellum. However, recent evidence indicates that motor adaptation also involves model-free learn
explicit strategy learning. Using rotation paradigms, here we demonstrate that savings (faster relearning), which is closely re
model-free learning and explicit strategy learning, is also direction specific. However, this new direction specificity can be abolish
the participants receive exposure to the generalization directions via an irrelevant visuomotor gain-learning task. Control ev
indicates that this exposure effect is weakened when direction error signals are absent during gain learning. Therefore, the d
specificity in visuomotor learning is not solely related to model-based learning; it may also result from the impeded express
model-free learning and explicit strategy learning with untrained directions. Our findings provide new insights into the mecha
underlying motor learning, and may have important implications for practical applications such as motor rehabilitation.

Key words: learning specificity; motor adaptation; motor generalization; motor learning

Significance Statement

Motor learning is more useful if it generalizes to untrained scenarios when needed, especially for sports training and mo
rehabilitation. However, as a form of motor learning, motor adaptation is typically direction specific. Here we first show tha
savings with motor adaptation, an index for model-free learning and explicit strategy learning in motor learning, is also directio
specific. However, the participantsÕ additional exposure to untrained directions via an irrelevant gain-learning task can enabl
complete generalization of learning. Our findings challenge existing models of motor generalization and may have import
implications for practical applications.

ntroduction

Learning will not be very meaningful if it is confined to its original learning context. Motor learning generalization examines how learning in one context influences the performance in untrained contexts and offers a unique window for investigating the nature of motor learning (Poggio and Bizzi, 2004; Shadmehr, 2004). Adaptation paradigms have been frequently used to study motor learning generalization in the context of reaching, where arm movements are systematically perturbed by visual distortion (Pine et al., 1996; Bock et al., 2001) or robotic forces (Thoroughman and Shadmehr, 2000). Typically, learning obtained with adaptation paradigms in one part of the workspace is not fully generalizable to other parts of the workspace when examined with aftereffects (Krakauer et al., 2000; Wigmore et al., 2002; Donchin et al., 2003; Wang and Sainburg, 2004; Krakauer et al., 2006). A widely accepted view is that learning leads to the formation of internal models, a conceptual construct of how the nervous system predicts the sensory consequence of motor commands in the face of perturbations (Shadmehr et al., 2010). The generalization of this learned construct is thought to be constrained by learning-related changes of tuning properties in lower motor cortices, including the primary motor cortex (Thoroughman and Shadmehr, 2000; Paz et al., 2003), the cerebellum (Shadmehr et al., 2010), and the premotor cortex (Wise et al., 1998; Krakauer et al., 2004).

However, recent findings suggest that motor adaptation, which is traditionally attributed to internal models and cerebellum-based learning, consists of model-free learning components (Diedrichsen et al., 2010; Huang et al., 2011; Verstynen and Sabes, 2011; Shmuelof

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et al., 2012) and explicit strategy-learning components (Taylor et al., 2014; McDou[redacted]al., 2015). Wh[redacted]se parts of learning are subject to direction specificity is unknown. To investigate this issue, we have to abandon the conventionally used aftereffects and instead use savings (i.e., faster relearning during delayed retest) as the generalization index. In contrast to aftereffect, which reflects the combined effect of all learning components, savings is a behavioral marker for model-free learning and explicit strategy learning (Huang et al., 2011; Haith et al., 2015). Furthermore, savings is a universal metric for all learning systems, including semantic, perceptual, and motor systems (E(p.4(rcepasjrning)91 k [())y/ab21.5 04BT 9.5 0 0 9.5 123.195 396.7273 Tm 0 0 0 1 k 0 Tc (;)Tj ET /2242.3s BT

Experimental design

Experiment 1 (generalization without exposure). Each participant was trained at one of the four possible directions (either 0°, 45°, 90°, or 135°) but was tested at the same generalization direction (0°). They were randomly assigned to one of these four training groups. The experiment consisted of the following four consecutive phases: familiarization, baseline, training, and generalization (Fig. 1*B*). During the familiarization phase, each participant moved to the training and the generalization targets with veridical and continuous cursor feedback. Each target was visited 10 times, and the order of the targets was randomized. The baseline phase was identical to the familiarization phase except that only the end-point position of the cursor was displayed. This phase was to establish participants movement baseline for moving toward these targets with end-point feedback. In the training phase, the participants moved to the training target 80 times with visuomotor rotation imposed. The feedback was provided at the end point only. In the generalization phase, the participants moved to the 0° target 80 times with the same perturbation and end-point feedback as for evaluation of the savings. These four groups were labeled as No-Exposure groups (see below).

Experiment 2 (generalization enabled by visuomotor gain learning). Another three groups of participants (Gain-Exposure groups) were tested for the effect of a secondary gain-learning task on motor generalization. The procedure was the same as that in Experiment 1, except that there was a brief exposure phase between the training and generalization phases. Each group was trained for a single direction at 45°, 90°, or 135°. During the exposure phase, the participants moved 20 times to the 0° generalization target with visuomotor gain perturbation. Gain learning and rotation learning are distinct learning processes, as they are governed by different neural substrates (Turner et al., 2003; Krakauer et al., 2004) and can be obtained independently and concurrently (Yin and Wei, 2014). The gain between the actual movement and its display was set at 0.6 (a veridical gain was 1), while the direction feedback was veridical. Therefore, the participants should move 42 mm for the visually 70 mm away target to compensate for the imposed gain. After the exposure phase, all groups were tested again for their generalization at the 0° direction. To exclude the possibility that the exposure task alone could lead to generalization of rotation learning, a control group skipped the initial training phase, and completed only the exposure and generalization phases.

Washout controls (savings after washout). Experiments 1 and 2 showed that savings was direction specific and that it could fully generalize after the direction exposure (see Results). However, the aftereffect of initial training was not brought to baseline at the training direction. We thus repeated Experiments 1 and 2 but inserted a washout phase after the initial training. The washout phase included 40 reaching trials to the initial training target with veridical end-point feedback and no rotation perturbation. Similar to Experiment 1, three groups of participants were trained for 80 rotation trials at 0°, 45°, and 135°, respectively. After washout, they were tested at the generalization direction of 0°. In addition, similar to Experiment 2, another three groups of participants were trained at 0°, 45°, and 135°. They then completed a washout phase at the training direction and an exposure phase (i.e., gain learning) at the generalization direction before the generalization test.

Experiment 3 (relevant factors in the exposure task). To investigate the possible influences that could contribute to exposure-enabled generalization, six groups of participants completed different exposure tasks. The procedure was identical to that of Experiment 2 except that the exposure task varied, and only generalization at 135° was examined.

The first group (the Time group) examined whether the elapsed time was responsible for exposure-enabled generalization. Between the training and generalization phases, the participants sat idle for 1 min, approximately the same duration as in the original exposure task.

The second group (the Attention group) examined whether merely attending to the generalization direction could enable learning generalization. During the exposure phase, the participants performed a luminance discrimination task around the 0° generalization target. This visual task demanded that the participants direct their attention to the generalization direction. The task followed a single-trial two-alternative forced-choice staircase procedure for measuring discrimination thresholds. In each trial, two squares symmetrically flanked the 0° target (target not shown) with a randomly chosen deviation of 20°, 40°, or 60°. The participants were asked to verbally report which square (left or right) was brighter as quickly as possible. This arrangement forced the participants to visually attend to the area surrounding the generalization target. The experimenter pushed the left or right arrow key to record the responses. A classic 3-down-1-up staircase rule was used with a step size of 4 in a 256 grayscale. The reference luminance was at the 128th level of the grayscale. This exposure task lasted for ~60 s, similar to the duration of the visuomotor gain-learning task in Experiment 2.

The third group (the Tracking group) examined whether the exposure of a motor learning task without reaching movements could also enable generalization. The participants were required to track a moving visual target with the hand cursor as accurately as possible. The movement of the target followed a predefined figure-eight trajectory consisting of two identical ellipses whose two semiaxes were 18 and 5.7 mm long. The long axes of the two ellipses were aligned with the 0° target direction. This tracking task typically lasted for 120 s. To facilitate learning, the tracking error within a trial was calculated and presented to the participants after each trial. The tracking error was defined as the root mean square error of the tracking trajectory relative to the target trajectory, as follows:

$$\text{RMSE} = \sqrt{\left(\sum_{i=1}^{n}\Delta x^2 + \sum_{i=1}^{n}\Delta y^2\right)/n},$$

where Δx and Δy were the tracking errors in x- and y-coordinates in the screen unit, and RMSE was the root mean squared error. Tong and Flanagan (2003) reported no between-task interferences when a tracking task and a reaching task were successively learned with opposite visuomotor rotations. This result suggests that the memory resources for visuomotor rotations are task specific. It also implies that tracking and reaching are different tasks. Therefore, the performance of the Tracking group would indicate whether the exposure effect can be elicited by learning a motor task that is different from the original learning task.

The fourth group (the No-Feedback group) examined whether the exposure of similar reaching actions without visual feedback could enhance the relearning rate. The participants were required to make shooting movements toward the 0° generalization target without visual or reward feedback. Note that this straight-shooting movement involved identical muscle activation patterns as in the original rotation learning movements.

The fifth group (the Veridical group) examined whether the exposure of a reaching task with veridical feedback could facilitate relearning. The participants were required to make reaching movements toward the 0° generalization target with veridical visual feedback.

The sixth and last group (the Error-Clamp group) examined the potential effect of learning from small direction errors. During the exposure of gain learning, small direction errors still existed due to the end-point variance of natural reaching movements. In fact, people learn from their own small errors during unperturbed natural movements (van Beers, 2009). Here the directional errors were completely removed by using error-clamp trials where end-point feedback was projected onto the desired 0° movement direction.

Data analysis

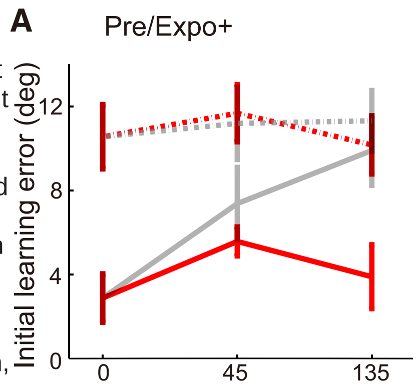
The direction error of hand reaching was used to quantify the performance in visuomotor rotation learning. The error was the angular difference between the desired direction (i.e., 30° clockwise from the target direction) and the actual movement direction. The latter was the direction of the vector between the starting position and the movement end point.

The error in the first generalization trial indicated the aftereffect. Though we did not remove the visual feedback as in previous studies, we only provided end-point feedback at the end of the trial. Thus, the directional error was still a valid indication of the participants feedforward estimate.

To quantify the savings, we first calculated the average errors over trials 2 9 in both training and generalization phases. The difference in errors between these two phases indicated changes in learning rate, with faster relearning signifying savings (for a similar treatment, see Krakauer

initial training at a distant direction to enable learning generalization.

The direction specificity and the effect of exposure persisted in the washout control conditions when the aftereffect of initial rotation learning was washed out. Three Non-Exposure groups first showed similar learning rates during initial training, and their relearning rates again showed direction specificity (Fig. 4*A*, gray). A direction × phase mixed-design ANOVA showed a significant main effect of phase (training vs generalization, $F_{(1,33)} = 13.65$, $p < 0.001$) and a significant interaction effect ($F_{(2,33)} = 3.70$, $p < 0.05$). The main effect of direction was not significant ($F_{(2,33)} = 2.24$, $p = 0.123$). Simple main effects showed no difference among directions in the training phase. In contrast, in the generalization phase, the learning rate decreased with angular separation: the 0° group had significantly faster learning than the 135° group ($p < 0.005$), but the 45° group was not significantly different from the 0° and 135° groups ($p = 0.067$ and 0.215). The savings were 25.6 ± 6.2%, 12.7 ± 7.6%, and 1.6 ± 4.5%, respectively, for the 0°, 45°, and 135° directions (Fig. 4*B*; one-way ANOVA, $F_{(2,33)} = 3.70$, $p < 0.05$). *Post hoc* pairwise comparison yielded a significant difference between the 0° and 135° groups ($p < 0.01$). Hence, we demonstrated direction specificity of savings after washout.



Importantly, in another three groups with exposure to the generalization direction, the direction specificity was again removed. A mixed-design ANOVA was performed with group (previous 0° No-Exposure group vs two Gain-Exposure groups) as a between-subject factor and phase (training vs generalization phases) as a within-subject factor. The results showed no significant main effect of group ($F_{(2,33)} = 0.81$, $p = 0.49$), a significant main effect of phase ($F_{(1,33)} = 62.49$, $p < 0.001$), and no significant interaction effect ($F_{(2,33)} = 0.35$, $p = 0.71$). Therefore, the exposure enabled full generalization after washout (Fig. 4*A*). This complete generalization was further confirmed by directly analyzing the savings (Fig. 4*B*). The savings of two Gain-Exposure groups at 45° and 135° were 20.3 ± 3.7% and 20.9 ± 4.5%, respectively, which were not significantly different from the savings of the 0° No-Exposure group ($F_{(2,44)} = 0.35$, $p = 0.71$). Therefore, washout of initial learning did not change the results observed in Experiments 1 and 2: savings exhibited direction specificity that could be removed by exposure to the generalization direction via a secondary gain-learning task.

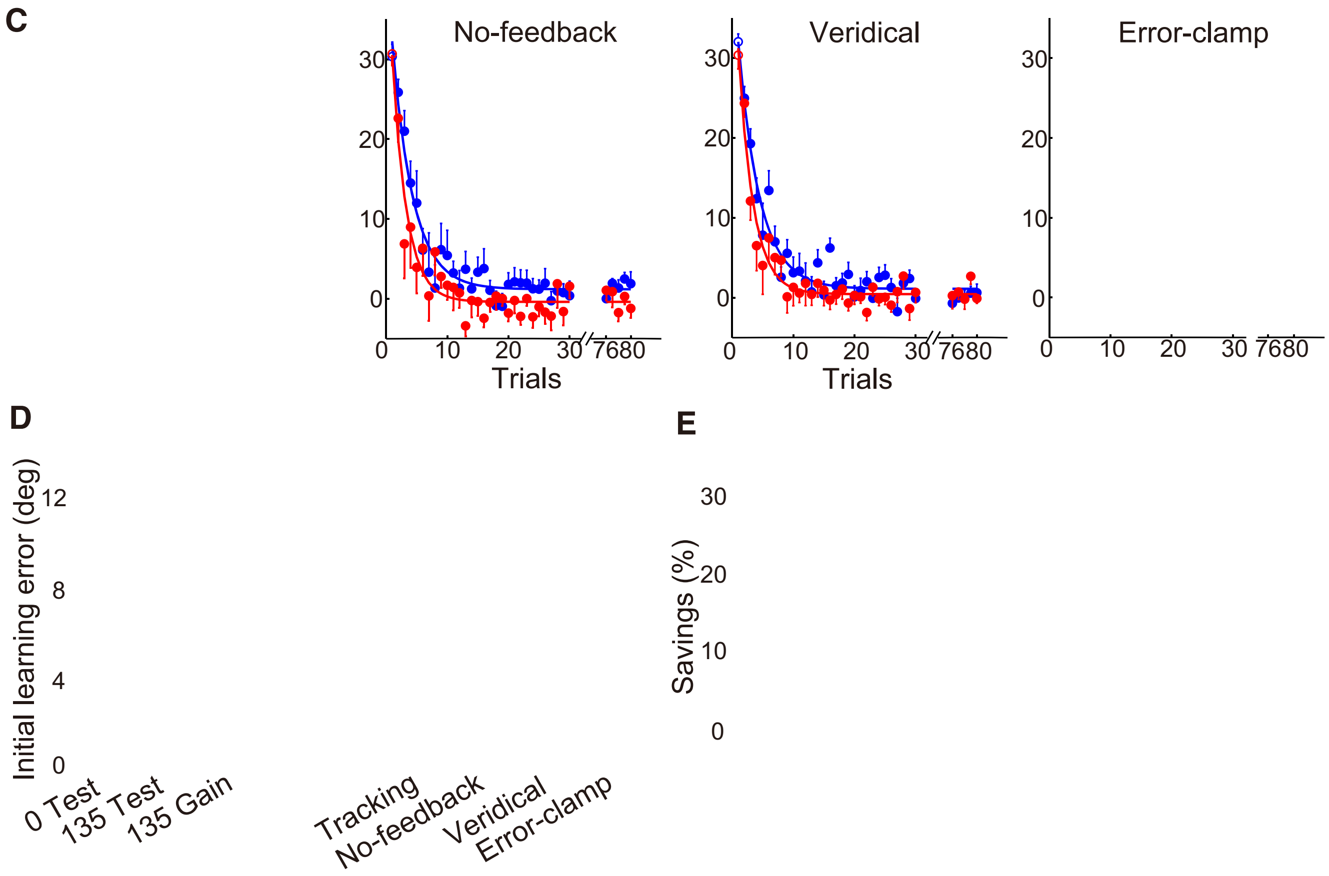
To understand why direction exposure enabled generalization, six groups of participants each completed a different exposure task (the Attention, Time, Tracking, No-Feedback, Veridical, and Error-Clamp groups; see Materials and Methods). The separation was 135°, where the enhancement effect was most apparent in the previous Gain-Exposure task (Fig. 5). Proper visual attention to the generalization direction by the Attention group was indicated by luminance discrimination learning (Fig. 5*A*). Similarly, active engagement of the tracking task by the Tracking group was indicated by tracking learning (Fig. 5*B*).

All of these groups started off with similar initial learning rates (Fig. 5*C*,*D*). Their initial learning errors were not significantly different from those of the previous 135° No-Exposure group and 135° Gain-Exposure group ($F_{(7,88)} = 0.15$, $p = 0.99$). These groups then performed different exposure tasks. In the generalization phase, their learning was again tested against the 135° No-Exposure group and 135° Gain-Exposure group, and a significant difference was found ($F_{(7,88)} = 2.45$, $p < 0.05$). *Post hoc* LSD tests revealed that these groups learned significantly more slowly than the original 135° Gain-Exposure group since the only difference was between the 135° Gain-Exposure group and other groups ($p = 0.007$, 0.001, 0.001, 0.006, 0.028, 0.028, and 0.056, respectively, when compared with the 135° No-Exposure, Attention, Time, Tracking, No-Feedback, Veridical and Error-Clamp groups). Only the Gain-Exposure group and the Error-Clamp group had significant savings ($t_{(11)} = 6.22$ and 2.48, and $p < 0.001$ and $p < 0.05$, respectively), and the Veridical group had marginally significant savings ($t_{(11)} = 2.09$, $p = 0.06$). The savings of the Time, Attention, Tracking, and No-Feedback groups were not significantly different from zero ($t_{(11)} = -0.09$, -0.02, 1.3, and 0.89, $p = 0.93$, 0.99, 0.22, and 0.39, respectively). We did not run a two-way ANOVA, given that these groups were independently sampled and the number of groups was large, thus the error variance was inflated.

Discussion

Our study demonstrates that savings in visuomotor rotation learning, like the aftereffect, is direction specific. This new direction specificity persisted after a washout session that brought initial learning back to the baseline before relearning. Interestingly, direction exposure with a visuomotor gain-learning task enables savings to fully generalize to distant directions. Control conditions showed that gain learning with no directional error feedback, and reaching with veridical feedback but without gain learning, lead to partial generalization. Thus, exposure to learning and direction errors may be necessary for full generalization of original rotation learning.

Motor generalization is traditionally indicated by the aftereffects, which exhibit direction specificity. This behavioral generalization function has been linked to neuronal tuning properties in primary motor cortices such as M1 and the cerebellum (Donchin et al., 2003; Paz et al., 2003; Shadmehr, 2004). More recent reweighting models that combine the population-coding model and the state space model propose that learning changes the connections between fixed-tuning population neurons with error signals (Poggio and Bizzi, 2004; Tanaka et al., 2009). In this latter framework, motor learning and generalization are manifestations of these weight changes, which are incrementally altered



by error signals. Thus, these generalization models are based on the concept of internal models and the measurement of aftereffects.

In contrast, savings reflects distinct learning components of motor adaptation, including reinforcement learning (Huang et al., 2011) and explicit strategy learning (Haith et al., 2015). Reinforcement learning, a form of model-free learning, is an operant association between the adapted movement and the successful error reduction (Diedrichsen et al., 2010; Huang et al., 2011; Verstynen and Sabes, 2011; Shmuelof et al., 2012). From a different perspective, motor adaptation is also divided into an explicit component, which is closely related to cognitive strategies, and an implicit component (Anguera et al., 2010; Fernandez-Ruiz et al., 2011; Taylor et al., 2014; McDougle et al., 2015).

The direction specificity of savings may reflect fundamental constraints on cognitive strategy and operant reinforcement acquired during motor adaptation. In this light, the nervous system has difficulty in applying a newly acquired cognitive strategy (e.g., aiming to a rotated direction) or a reinforced action (adaptive rotation for direction errors) to distant directions. We cannot distinguish between these two possibilities as they may be conceptually equivalent, both referring to an aiming strategy in the face of directional perturbations. Requiring the participants to explicitly report the aiming direction may help distinguish the explicit strategy from other learning components (Taylor et al., 2014). Limited generalization is not unexpected, though. In an uncertain environment, any task is associated with a large solution space of possible actions; and the nervous system shall not completely generalize the acquired control policy to any novel situation. The constraints for generalizing motor learning, especially those tied to reinforcement learning and cognitive strategy, demand further investigations.

The intriguing finding is that direction exposure with a seemingly irrelevant learning task can lead to full generalization. Similar muscle-activation patterns in the exposure tasks cannot account for this effect since both of those performed by the Tracking and the No-Feedback groups involve upper arm movements similar to those in the Gain-Exposure groups. In fact, the No-Feedback group used identical ballistic movements and muscle activations as the Gain-Exposure groups. However, neither the Tracking nor the No-Feedback group showed any generalization effect. Both gain learning with visual error clamp and simple reaching with veridical feedback induced partial generalization. Admittedly, reaching with veridical feedback also involves learning where people correct for their own motor errors (van Beers, 2009). We thus postulate that both learning and experiencing original error signals facilitate the nervous system to generalize the acquired strategy to new directions. The gain-learning task involves learning of a novel visuomotor map, a learning feature that also exists in the original rotation learning. Thus, direction exposure via gain learning may induce meta-learning, so that the nervous system infers that novel visuomotor mapping is applicable to a distant direction and consequently expedites the relearning of rotation. This possibility is consistent with recent findings that causal inference is an inherent component of motor learning (Wei and Körding, 2009).

In addition, experiencing directional errors, albeit small ones, can facilitate generalization. Savings has been related to heightened sensitivity to related movement errors (Herzfeld et al., 2014). Our exposure task may help the nervous system quickly recognize rotation errors and adapt to them more quickly during relearning. We also noticed that the first generalization trial, with or without exposure, showed no sign of aftereffect at distant directions. From this perspective, the nervous system may need at least one trial to probe the new direction before applying previously acquired learning (Klassen et al., 2005; Krakauer et al., 2005).

It is unlikely that the direction specificity of savings is caused by use-dependent learning, which is also a form of model-free learning. Use-dependent learning is a movement bias toward the adapted movement repeated at the learning asymptote. Thus, it can potentially lead to direction specificity if its influence decreases at distant directions. However, we found that after exposure to reaching movements 30° anti-clockwise from the desired solution (Gain-Exposure groups), savings can fully generalize. If use-dependent plasticity is at work, this exposure should only reduce generalization since the initial rotation training is 30° clockwise. Thus, consistent with a previous report that use-dependent plasticity is not sufficient for savings (Huang et al., 2011), our results suggest that the direction specificity of savings and its elimination are not related to use-dependent learning.

The exposure-induced motor generalization is in line with the transfer of visual perceptual learning enabled by a training-plus-exposure paradigm (Xiao et al., 2008; Zhang et al., 2010; Wang et al., 2012, 2016; Zhang and Yang, 2014). Perceptual learning becomes completely transferrable to untrained conditions after additional exposure of these conditions via an irrelevant task. These findings challenge perceptual learning theories that rely on learning-induced plasticity in early visual cortices (Karni and Sagi, 1993; Schoups et al., 1995; Teich and Qian, 2003). Similarly, low-level neural circuits in the primary motor cortex and the cerebellum have been assumed to constrain the generalization of motor learning across directions (Thoroughman and Shadmehr, 2000; Donchin et al., 2003; Paz et al., 2003; Shadmehr, 2004). Based on our findings, we suggest that motor generalization should also engage an extensive range of brain regions, including the striatum and the prefrontal and parietal cortices, which are closely related to reinforcement learning and cognitive learning (Tanaka et al., 2009; Anguera et al., 2010; Wachter et al., 2010).

Our findings are also in line with previous reports about the top-down influence on the generalization of motor learning. For instance, prior motor experience (Krakauer et al., 2006; Wei et al., 2014) and the participants' familiarity with the learning materials (Yan et al., 2013) can enhance the generalization, which was indexed by aftereffects. Note that these studies indicate that the enhancement in generalization is typically associated with long-term exposure of the same or similar learning tasks. For instance, daily experience with a computer mouse leads to enhanced generalization of visuomotor gain learning (Wei et al., 2014). The mouse use and visuomotor gain learning share similar visuomotor transformation, in which the gain between the movement and its visual representation is modified from the veridical one-to-one mapping. Our current study goes further to show that learning can completely generalize to distant directions with a brief exposure via an irrelevant learning task.

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