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Generalization of unconstrained reaching with hand weight changes

***Running head*: generalization of familiar perturbations**

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Abstract

Studies of motor generalization usually perturb hand reaches either by distorting visual feedback with virtual reality or by applying forces with a robotic manipulandum. While such perturbations are useful for studying how the central nervous system adapts and generalizes to novel dynamics, they are rarely encountered in daily life. The most common perturbations that we experience are changes in the weights of objects that we hold. Here we use a center-out, free reaching task in which we can manipulate the weight of a participant's hand to examine adaptation and generalization following naturalistic perturbations. In both trial-by-trial paradigms and block-based paradigms we find that learning converges rapidly (on a timescale of ~2 trials) and this learning generalizes mostly to movements in nearby directions with a uni-modal pattern. However, contrary to studies using more artificial perturbations, we find that the generalization has a strong global component. Furthermore, the generalization is enhanced with repeated exposure of the same perturbation. These results suggest that the familiarity of a perturbation is a major factor in movement generalization, and that several theories of the neural control of movement, based on perturbations applied by robots or in virtual reality, may need to be extended by incorporating prior influence that is characterized by the familiarity of the perturbation.

Key words: motor generalization, familiarity, reaching movements, state space model, generalization function

INTRODUCTION

As we move and interact with the environment we constantly update our sensorimotor behaviors to adapt to changing sensory feedback and forces on our limbs. Which aspects of these changes are learned and how these changes are represented in the nervous system have been extensively studied by examining how people generalize a behavior learned in one context to another. Traditionally, generalization studies have perturbed reaching movements by introducing visual distortion in a virtual reality setting (e.g., Bock 1992; Ghahramani et al. 1996; Imamizu et al. 1995; Mattar and Ostry 2007; Paz et al. 2003) or by applying deflecting forces with robots (e.g., Donchin et al. 2003; Shadmehr and Mussa-Ivaldi 1994; Sing et al. 2009; Thoroughman and Shadmehr 2000). Participants usually adapt to these perturbations within a training session and generalization is assessed by having participants make reaches with different joint configurations, spatial locations, effectors, or movement directions. Under these conditions behavior often generalizes locally to contexts that are similar to the training condition (Shadmehr 2004). This is not surprising, from a normative view, since the novel perturbations employed in these laboratory settings are rarely encountered in our daily life and the perturbations applied in a short experimental session might not be applicable to other contexts. If a perturbation is frequently experienced in daily life, can the nervous system generalize it easily and to widely varying contexts? How we generalize familiar perturbations has not been systematically examined.

For most types of perturbations, previous studies have found that generalization of planar reaching movements peaks around the training direction and decays with increasing angular separation from the training direction. For instance, force field learning generalizes minimally beyond 90° (Donchin et al. 2003; Mattar and Ostry 2007), while learning of visuomotor rotations exhibits even narrower generalization, only to targets within ~45° (e.g., Krakauer et al. 2000). In some cases, the degree of direction-dependence may indicate how learning occurs and how perturbations might be represented in the brain. Generalization curves are often associated with the tuning properties of neurons in various brain areas. For example, neuropsychological, electrophysiological, and imaging studies have found that learning of visuomotor rotations is associated with changes in the cerebellum (Krakauer et al. 2004; Rabe et al. 2009; Tseng et al. 2007), ventral premotor cortex (Krakauer et al. 2004), primary motor cortex (Paz et al. 2003; Wise et al. 1998) and posterior parietal motor cortex (Diedrichsen et al. 2005; Inoue et al. 1997). Most theories emphasize a bottom-up view where sensory errors lead to a reorganization of neural primitives and their connections which directly determine generalization that is behaviorally observed (Poggio and Bizzi 2004; Tanaka et al. 2009; Thoroughman and Shadmehr 2000). Here we postulate that generalization is also under top-down influence where familiarity with the perturbation impacts generalization, in analogy to the way that prior experience biases percepts in various perceptual systems (e.g., Mamassian and Goutcher 2001; Stocker and Simoncelli 2006). Our working hypothesis is that familiar perturbations should lead to more global generalization than that previously found when participants learn less familiar perturbations created by virtual reality feedback or robots.

Here we investigate motor generalization with a novel experimental paradigm in which the weight of the participant's hand can be unexpectedly modified during center-out reaching. This paradigm allows us to impose naturalistic perturbations, similar to those experienced as we move objects of varying weights. By naturalistic perturbations, we mean that the perturbation is not generated by virtual reality or robot-generated deflecting forces as they are rarely encountered in our daily life. Hand weight changes are common perturbations to the nervous system. For example, to transport a cup of coffee to our mouth, for instance, our nervous system needs to tailor motor commands according to the cup's weight. When we take a sip or add more coffee to the cup the weight changes and our motor commands must be updated to compensate. Here we found that generalization to this type of familiar, naturalistic perturbation is global and unimodal across directions. Repeated exposure to the perturbation enhances this broad generalization, in contrast to other types of perturbations where repeated exposure does not change generalization or results in a narrowing of generalization (Donchin et al. 2003; Krakauer et al. 2000; Mattar and Ostry 2007; Tanaka et al. 2009; Thoroughman and Shadmehr 2000). These findings support our normative hypothesis and suggest that bottom-up explanations of generalization using neural tuning should be complemented with top-down mechanisms involving prior experience.

METHODS

Apparatus

Participants were seated in front of a desk with a light paper box (~10g) firmly attached underneath the right hand (Figure 1). A water-filled plastic bag was placed in the box and connected to a syringe (140g capacity) through a 2.2 m light-weight plastic tube running underneath the arm. Sitting behind the participant, the experimenter could change the weight of the participant’s hand by injecting/removing water from the plastic bag with the syringe. A plastic palm brace was placed between the water box and the palm to minimize tactile cues, and participants wore noise-isolating biauricular headphones throughout the experiment to block possible auditory cues during weight changes. These procedures prevented participants from noticing changes in the weight of the hand between trials, while their hand rested on the support (a 10.5cm high, 3.0cm diameter cylinder fixed on the desk top) before each movement. The hand, the water box, and the palm brace were all wrapped together with medical bandage such that they could be treated as a rigid body. The pointed index finger was fixed on the palm brace and fingertip location was measured throughout the experiment by an attached IR marker (Codamotion, Charnwood Dynamics; sampling rate at ~200Hz).

Before each trial the participant rested his/her right hand on the support. With the tip of the index finger as a center, five red LED targets (15 cm above the desk top and separated 45° apart) were placed on a 20-cm perimeter. The LED targets were at the same height as the finger tip given the height of the support. The basic task was to move the fingertip from the starting position to one of the LED targets. The illumination of a LED light was controlled by a programmable circuit board (Arduino Duemilanove). After each reach, to facilitate the participant's return to the starting position in 3D space, the finger position was displayed as a cursor (1.5cm in diameter) on a projection screen (projector model OPTOMA EX774) 1.5 meters in front of the desk. A red circle (2.5 cm in diameter) was also displayed on the projection screen to indicate the starting position. When the distance between the actual finger tip and the starting position was less than 1.0 cm, the starting circle expanded to a red disc (5.0 cm in diameter) to notify the participant that the finger tip was in place. Participants subsequently attended to the table and waited for a LED target to be lit up. Data acquisition and screen display were controlled by a customized Matlab program (Matlab 2009b).

Basic Movement

Participants performed center-out, unsupported, point-to-point reaching movements to each of the 5 targets with varying hand weight. Each trial started off when participants placed their right hand on the hand support and aligned the index finger with the starting position. Once the hand was properly placed, the monitor of the data-acquisition computer, unseen by the participant, displayed an instruction to the experimenter who sat behind the participant. The instruction signaled the experimenter to inject or remove water using the syringe. Upon finishing water change, the experimenter pressed the space key on a wireless keyboard to light up one of the LED targets, signaling the participant to initiate a reach. Participants were instructed to move quickly and comfortably to the LED target with precision and hold at the target position briefly until the LED was off. Then participants returned the hand to the starting position for the next trial. If the index finger was within 1.1cm of the target, a monetary reward of 2 cents would be displayed on the projection screen to motivate participants. The hand movement from the starting position to the target usually lasted 800~900ms and the trial-to-trial interval was about 2.6±1.7s (including the movement time and the resting time on the hand support). To prevent slow movements, we would warn participants with a sharp beep played by a loudspeaker if a reach lasted longer than 900ms.

Protocols

Experiment 1 employed trial-by-trial weight changes to perturb reaching movements. Each trial was randomly assigned with a target direction and a hand weight, with the hand either loaded with 140g water (heavy condition, *H*) or without (light condition, *L*; the water bag with its containing box has a dead weight of about 37 grams without water load). Thus each trial is associated with one of 4 types of weight transitions, depending on the loading on the current trial and the immediately proceeding trial: heavy to light (*H2L*), light to heavy (*L2H*), light to light (*L2L*) and heavy to heavy (*H2H*). Defining the leftmost target as 0° and the rightmost target as 180°, the angular separation between two successive trials could take one of 9 values: 0, ±45°, ±90°, ±135°, and ±180°. Before the experiment, participants were familiarized with the setup by practicing reaches without weight changes. The formal data collection consisted of 5 (targets) × 4 (weight transitions) × 50 (repetitions) = 1000 trials. The experiment lasted about 90 minutes with a 10-minute mandatory break after the 500th trial. It should be noted that although each target was equally likely the angular separations between trials were unevenly distributed: 0° separation was presented most frequently while ±180° were least likely. On average, 0°, ±45°, ±90°, ±135°, and ±180° transitions should occur for 200, 320, 240, 160 and 80 times, respectively. As the target sequence was fully randomized in the experiment, actual numbers were slightly different.

Experiment 2 investigated block-based learning and generalization. Participants first learned to reach the same target with loading (H) for a number of trials. Immediately after this block learning, generalization was assessed by a test trial when participants reached to other directions with or without loading. These training trials and the subsequent test trial were counted as a block. This block-design or postadaptation-design experiment had two-day data collection: on one day participants were trained to reach to the target at 0° and on the other day at 180°. As such the 0° training led to generalization to all positive angular separations (0, 45°, 90°, 135°, and 180°) and the 180° training to corresponding negative angular separations. Data collection on each day was further divided into three sessions that involved different lengths of training. In 2-trial learning session (called Block2), the average number of training trials is two: 20% of the blocks had one training trial, 20% had three trials and 60% had two trials. The same training-length distribution was applied to 4-trial and 6-trial sessions (called Block4 and Block6; e.g., Block4 sessions consists of 20% 3-trial, 60% 4-trial and 20% 6-trial blocks). The aim of this design was to investigate whether learning and generalization of hand weight changes can be modulated by length of exposure. The orders of training directions (days) and of training length (sessions) were counter-balanced and randomly assigned across participants.

Each session started with a block of 30 unloaded trials (washout block, 6 trials each target) to familiarize the participant with the apparatus and to wash out the effect from previous sessions. The rest of the session consisted of 50 blocks of trials: in each block participants first reached for a single target repetitively with loading and then they were tested by reaching for one of the 5 targets. The 2-trial learning session had 30 (washout block) + 3 (averagely 2 training and 1 test trial in a block) × 50 (blocks) = 180 trials. The 4-trial and 6-trial learning sessions had 280 and 380 trials, respectively.

As 8 participants (out of 11) were tested in both Experiment 1 and 2, there is a possible carry-over effect between experiments. To rule out this possible confound, we performed a control experiment with the same protocol as in Experiment 1 but with a new set of 9 participants. The only difference was that the finger position was sampled at 100 Hz by an infrared motion capture system (Optitrack, model V100:R2).

Participants

Both main experiments had 11 volunteer participants and 8 of them were tested in both experiments. The average age of two participant groups was 21.9±1.6 and 22.3±1.8, respectively. The number of male participant was 6 and 7, respectively. All eight, shared participants were examined for Experiment 2 first. The control experiment had a separate group of 9 participants (age 21.8±2.0; 4 males). All participants provided informed consent before data collection and they were naive to the purpose of the experiments. One participant in Experiment 1 and two participants in Experiment 2 were left-handed but they reached with the right hand. All participants had normal or corrected-to-normal vision. All procedures were approved by the ethics committee of Peking University.

Data Analysis

Changes in the weight of the hand primarily affect the vertical displacement of the hand during reaching (Figure 1B & C). Reaches were essentially horizontal towards the target if the hand weight was not changed from the previous trial. However, when the weight was changed unexpectedly the movement trajectory was either elevated or lowered depending on whether participants expected their hand to be heavier or lighter, respectively. Denoting trial types by the current and preceding hand weight, trials without weight changes are labeled as *H2H* and *L2L* and trials with unexpected weight changes as *H2L* and *L2H*. Changes in trajectory height thus represented an estimation error in hand weight and can be used to assess learning and generalization. An alternative way to quantify the influence of weight changes is to compute the peak height, either upward or downward, within a certain window of the hand trajectory. However, we noticed that a large portion of trials did not have a clear peak height in the mid of the trajectory (especially for *L2H, H2H* and *L2L* trials; see Figure 1C). Hence, it is best to use average height as the independent variable as it captures the main effect of unexpected weight changes, independent of the specific shape of a trajectory. Before calculating the average height, the trajectories between 10mm and 180mm were interpolated to 100 data points. The first 10mm of movement was omitted due to jitter of hand on the hand support during the reaction time period (the support has a radius of 10mm), which made interpolation for some trials impossible. The last 20mm of movement was also excluded, since, for some trials, participants stopped movement early without reaching the full, required distance of 20cm. The last segment also tends to be less indicative of weight-related feed-forward learning, since participants tend to home in on the target and make small corrective movements at the end of the reach (Figure 1C).

In Experiment 1, learning of weight changes can be quantified by calculating the differences in height between different types of trials. The difference between *L2H* and *H2H* indicates how much is learned about an empty load, and the difference between *L2L* and *H2L* indicates how much is learned about a full load. In each pair of comparisons the current reach has same load but differs in terms of the immediately preceding load. Hence their difference can be attributed to influence of the preceding exposure. We further grouped these differences by angular separations between pairs of trials, allowing us to quantify directional generalization (see eq. 1 & 2 below). In Experiment 1, two directional generalization functions (learning loading: *L2L* – *H2L*; learning unloading: *H2H* – *L2H*) can be derived for learning an empty load and a full load, respectively.

Experiment 2 mainly investigated the learning and generalization of a full load and we are thus interested in the difference between *L2L* and *H2L* trials. The last 5 trials in the washout block (without loading) were used to estimate the height of *L2L*. The test trials without loading were used to estimate *H2L*. Thus the generalization function (*L2L* – *H2L*) can be calculated.

To compare learning across directions, we need to consider directional biases caused by the inertial anisotropy of the limb (Flanagan and Lolley 2001; Gordon et al. 1994; Mussa-Ivaldi et al. 1985). This inertial bias means that the height difference, the behavior observable in our experiment, may be different across directions even when the weight estimation error is the same. This bias, directly related to limb *compliance*, can be estimated by taking the average height of trials with a weight transition but without a direction transition. For example, consider all the trial pairs that reach to the same direction but the first trial with load (*H*) and the next without (*L*). The average difference in heights can be viewed as a proxy for limb compliance in that direction, since it resulted from, on average, one unit of weight estimation error. This compliance measure is thus a 5 (direction) × 2 (weight change) matrix. In practice, we find that limb compliance is fairly consistent across participants (see results). We can then convert the observed height into a degree of learning (or generalization):

$$Learning_{unloading} = \frac{H2H - L2H}{Compliance_{direction,unloading}} \quad (1)$$

&

$$Learning_{loading} = \frac{L2L - H2L}{Compliance_{direction,loading}} \quad (2)$$

Taking learning loading as an example (eq.2), the *H2L* trial involves a loading transition where a heavy loading has been learnt in the previous trial but the current trial has no loading. The *L2L* is the average height in the same direction of the current trial and it serves as a baseline height for reaching without loading in this direction. The difference between *H2L* and *L2L* is thus caused by learning in the previous trial with loading. If this previous trial differs in direction than the current trial, then the computed learning is actually an estimate of directional generalization. It amounts to 1 if generalization is complete and 0 if no generalization happens. Note that compliance is measured for absolute targets directions, while generalization is estimated by dividing the compliance in the current target direction and it is a function of relative target directions (angular separations).

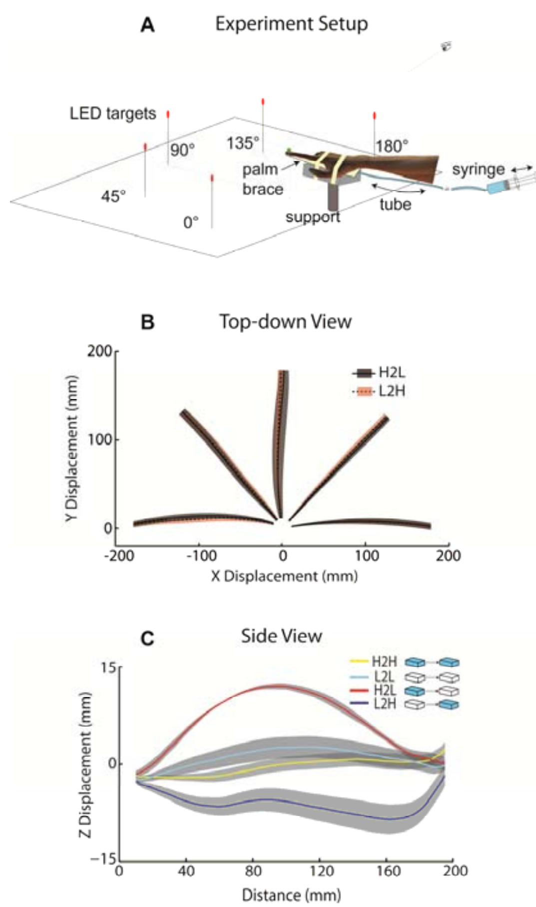

Figure 1: Experimental setup and exemplary trials. A) Experimental setup. Participants made cued, unconstrained reaches to five targets placed 15cm high, 20cm away from the starting position. Between each trial and without the participant's knowledge, the hand weight is modulated by changing a water load attached underneath the hand. Behind the participant, the

experimenter can change the volume of water and, thus, weight at the participant's hand using a syringe. B) A top-down view of movement trajectories. *H2L* and *L2H* trials are plotted for a typical participant in Experiment 1. The shaded area denotes ±1 SD across trials (same below). C) Trajectory height as a function of distance from the starting position for the same participant in Experiment 1 reaching for the 90° target with 0° angular separation between trials.

The Models

A state-space model was formulated to derive a generalization function based on trial-to-trial changes in trajectory height. We assume that the weight estimate on the *i*th trial (X_i) is influenced by the previous estimate (X_{i-1}) and the learning from the preceding trial:

$$X_i = X_{i-1} + G_{\theta_i,\theta_{i-1}}(X_{i-1} - W_{i-1}) \tag{3}$$

$$Y_i = A \times X_i \tag{4}$$

where W_{i-1} is the loading in the preceding trial which takes a value of 1 or -1 for a heavy or a light load, respectively. Thus $(X_{i-1} - W_{i-1})$ is the error in weight estimation experienced during the preceding trial. Note both X and W are 5×1 vectors to quantify simultaneous representations in 5 movement directions. $G_{\theta_i,\theta_{i-1}}$ captures the learning rate as a function of angular separation $(\theta_i - \theta_{i-1})$ and it is a 5×5 matrix. Originally there are 9 kinds of angular separations. However, we can reduce the number of free parameters in *G* from 9 to 5 by assuming that learning rates of negative angular separations are the same as those of corresponding positive separations. Finally, we include a scaling factor *A* to convert weight estimates into the observed hand height Y_i. The model (Model 1) is an autoregressive model of order 1. From the data we find that weight changes tend to be learned almost completely in a single trial, and including higher-order autoregressive terms does not significantly improve the model.

As a control, we also examined whether a flat generalization function might be sufficient to explain our data. In this case, learning only depends on the weight changes and is independent of any differences in target direction. Assuming that generalization is equal in all directions and that the current estimate is influenced by 4 immediately preceding trials, we can rewrite eq.3 as

$$X_i = X_{i-1} + \sum_{\Delta=1}^{4} L_{\Delta}(X_{\Delta} - W_{\Delta}) \tag{5}$$

where $L_{i-\Delta}$ and $(X_{i-\Delta} - W_{i-\Delta})$ are the learning rate and the error experienced Δ trials before the current trial, respectively. Thus the current estimate is affected by the immediate preceding estimate as well as influences from previous trials. As we are only interested in the relative contributions from previous trial, we set the learning rate as 1 for $\Delta = 1$ to reduce the number of parameters. This flat-generalization model (Model 2) is a standard state space model with 4 free parameters (three learning rates and, as in Model 1, a scaling factor *A* that maps the weight estimates to hand height).

We fitted the models with the trial sequence and trajectory heights (normalized by their corresponding compliance) from each participant in Experiment 1 to derive the generalization functions *G* (Model 1) or the learning rates *L* (Model 2). The data from Experiment 2 was not sufficient to constrain the model, since the longest trial sequence contained only 380 trials (Block6) and there were only 50 trials with weight changes. Active-set search algorithm (Matlab R2009, Mathworks) was used for model fitting.

RESULTS

Here we have constructed an experiment that allows us to change the effective weight of the hand by pumping water in and out of a brace that is attached to the hand. This allows us to analyze, using both trial-by-trial and block-based paradigms, how these naturalistic force perturbations are generalized.

Experiment 1: Trial-by-trial generalization

Despite the fact that changes in hand weight are unexpected, trajectories in the horizontal plane showed negligible differences (Figure 1B). The two types of weight-changing trials (*H2L* and *L2H*) are indistinguishable in the horizontal plane. However, during each trial participants learn about the weight of their hand, and this information affects the height of their trajectory on the next trial (Figure 1C). With unexpected loading (*L2H*), the hand moves lower than movements during an expected load (*H2H*). With unexpected unloading (*H2L*), the hand moves higher than movements during an expected load (*L2L*). Note that the conditions being compared (e.g., *L2H* v.s. *H2H*) always have an identical hand weight (e.g., both being heavy) and the differences in trajectory can be attributed to the weight and direction of the immediately preceding trial. These differences suggest that the hand weight from the previous reach biases the estimate of hand weight and subsequently impacts the next movement. Hence, when the hand weight is unexpectedly changed, the reach is substantially elevated or lowered.

Trial-by-trial learning of weight changes generalizes across directions (Figure 2A). The generalization function is mostly unimodal: the generalization is most prominent when moving in the same direction as the preceding trial and is gradually reduced with increasing angular separation. A 2 (type of generalization) × 5 (angle) two-way repeated measures ANOVA reveals a significant main effect on loading, indicating that generalization for learning loading (*H2H – L2H*) is larger than generalization for learning unloading (*H2L – L2L*). However, the interaction fails to reach significance ($p = .81$) suggesting that the two generalization functions tend to have the same pattern against angles. Examining the average generalization curve over these two generalization functions, we find that the generalization is significantly higher at 0° and 45° angular separations than those at 135° and 180° ($p < .05$, two-tailed paired-t tests). The generalization between the 90°, 135° and 180° angular differences are not significantly different ($p > .05$). On the other hand, the generalization is still significantly larger than zero even at the largest angular separation of 180° ($p < .05$), indicating a strong global generalization component.

The generalization function is also estimated by the state-space model (Model 1; Figure 2A). The model captures the overall height changes across trials with 40.2 ± 3.5% of variance explained (6 free parameters and 1000 data points) and it tracks trial-by-trial changes fairly well (Figure 2B). More importantly, the generalization function exhibits a similar semi-global unimodal pattern as in the data. Note the generalization function from the model is comparable to the average generalization (over both unloading and loading generalization curves) from the data since the model computes average learning from a previous trial disregarding of the sign of weight changes. A 2 (model v.s. data) × 5 (angle) two-way repeated measures ANOVA does not find significant main effect on the model-vs-data comparison or significant interaction, indicating a good match between model predictions and the data.

In contrast to the full generalization model (Model 1), Model 2 with a flat generalization function can account for only 27.7±3.1% of variance in the data. The learning rate drops rapidly with elapsed time; it appears that most of the learning happens within one trial (Figure 2C). We compared the performance of Model 1 and Model 2 using Bayesian Information Criterion (BIC, Schwarz 1978) in order to take different numbers of free parameters into account. Model 1 is significantly better than Model 2 with a reduction of 168.5±76.2 in BIC measures ($p < .0001$), indicating that a generalization function with direction dependency can better explain the data.

We find that the limb is more compliant during reaches to the target at 90° (where the hand is further from the body) than reaches to targets at 0° and 180° (where the hand is closer to the body). In general, reaching forward is more influenced by erroneously estimated hand weight than reaching laterally. Compliances for upward (unexpected unloading) and downward (unexpected loading) movements are not significantly different (Figure 2D). These findings are confirmed by a 2 (vertical direction) × 5 (horizontal direction) two-way repeated measures ANOVA where the main effect on horizontal direction is significant ($p < .0001$) but the main effect on vertical direction is not ($p = .16$). Similar direction-dependence was observed in Experiment 2 where a different set of participants were measured on different days (Figure 2D). This similarity between experiments suggests that our estimation of compliance is reliable.

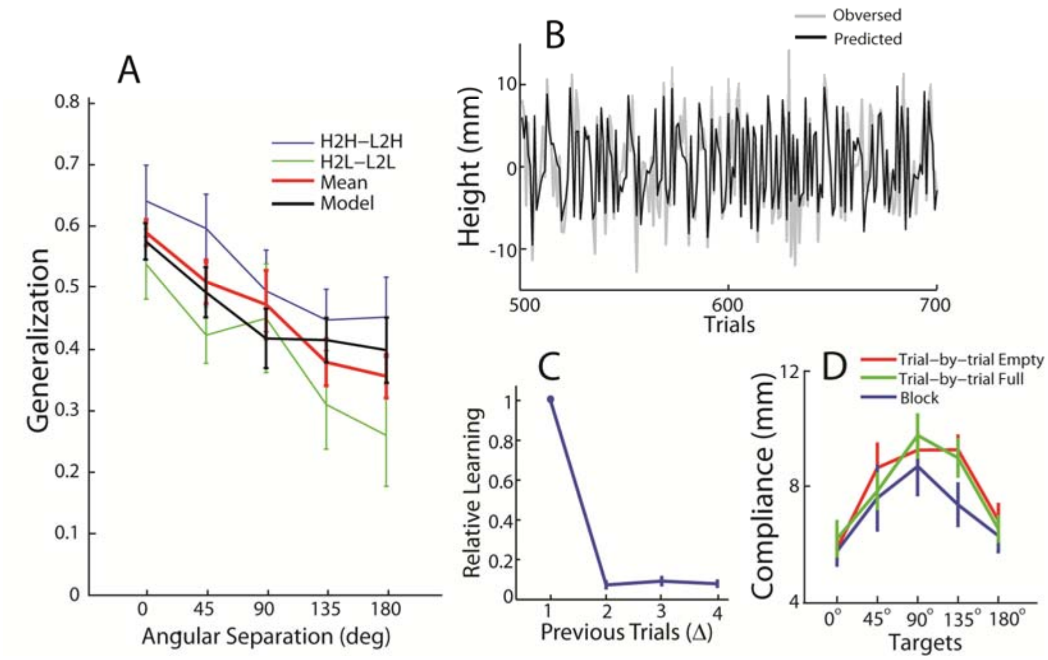

Figure 2: Results from Experiment 1 with trial-by-trial hand-weight perturbations. A). Generalization functions from learning loading (*H2H – L2H*) and unloading (*H2L – L2L*), the average across both conditions, and the corresponding model-predicted generalization function. Error bars denote standard errors across participants (same below). B). Trial-by-trial changes of trajectory height for a typical participant and the corresponding model predictions. C). The relative learning (L_{Δ}) from previous trials as estimated from Model 2. D). Compliance of vertical hand displacement as a function of movement direction. The compliance is estimated from unexpected loading and unloading trials from Experiment 1 and 2.

Experiment 2: block-based generalization

Repetitive exposure of the same load leads to a similar unimodal generalization pattern as in the trial-by-trial experiment (Figure 3A). Interestingly, different training lengths yield similar generalization, as a 3 (block size) × 5 (angle) two-way repeated measures ANOVA does not find significant main effect on block size ($p = .24$) or interaction ($p = .43$). We thus pool over data from three training-length conditions for the following analyses. Generalization is significant for all directions (paired t-test, $p < .0001$). The generalization at 0° and 45° are not significantly different from one ($p = .56$ and .08, respectively), indicating a full learning and generalization around the training direction. Paired t-tests indicate that the generalization pattern is uni-modal: generalization is significantly higher at 0° than at all other directions ($p < .05$), also higher at 45° than at 90° ($p < .05$), and it plateaus for other larger angles.

We examine how learning evolved over training trials (Figure 3B). Trajectory height increases at unexpected unloading trials and it is then substantially lowered at the first training trial with loading. Both trials are significantly different from other trials as indicated by paired-t tests. This sharp reversal is suggestive of one-trial learning from unexpected unloading. Participants manage to increase the height back to the baseline level in the next training trial as confirmed by paired-t test ($p > .05$). This fast learning is observed in all three training-length conditions. From another perspective, the learning from a single trial can also be viewed from the perspective of generalization: after experiencing an unexpected unloading in one direction (test trials), participants were tested in other directions (the training directions at 0° and 180°). By analyzing this first training trial after the test trial in each block, we can estimate a generalization function of de-adaptation embedded in the block paradigm (Figure 3C). This generalization pattern shows a unimodal pattern with a strong global component, remarkably similar to its counterpart in the trial-by-trial design (*H2H–L2H*). In fact, they are statistically indistinguishable (two-way ANOVA, $p = .53$ for main effect of experiments comparison). However, it is important to note that in this case the load was not entirely unexpected, since reaches to the training target always used the *H* condition.

The generalization functions from the block-based learning and the trial-by-trial learning of a reduced load are compared directly (Figure 3D). A 2 (experiment) × 5 (angle) two-way repeated measures ANOVA yields significant main effect on experiment ($p < .01$) and significant interaction ($p < .05$). These results indicate that more training in one direction tends to improve the overall generalization and this improvement is especially more pronounced around the training direction.

One confound for direct comparison between experiments is that eight participants were tested in both experiments. The exposure to weight changes during one experiment might affect their generalization in the second experiment. However, we think this carry-over effect is less likely given that the learning and its washout happen promptly on a time scale of 1 or 2 trials (Figure 3B). Nevertheless, we performed a control experiment with a new set of 9 participants with an identical protocol as in Experiment 1. We find that the generalization function is similar to the one found in Experiment 1 (Figure 3D). A 2 (experiment) × 5 (angle) two-way repeated measures ANOVA fails to find significant difference between experiments (main effect $p = 0.73$). This result suggests that generalization of adaptation to weight changes is not affected by a short session of exposure to weight perturbations.

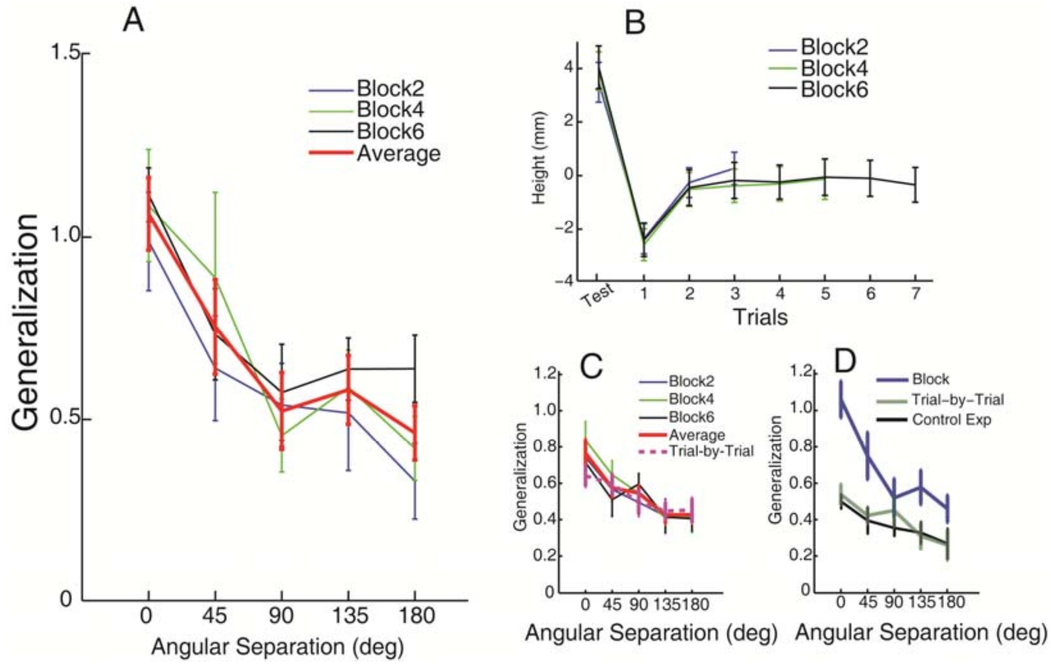

Figure 3: Results from Experiment 2 with block-based training. A). Generalization functions for unexpected unloading following training with 2 trials, 4 trials, 6 trials and their average. B). Trajectory heights within a training block with its preceding unloading trial. Blocks with different training lengths are plotted separated. C). Similar generalization functions as in A) but associated with the loading immediately following the unloaded test trials, i.e., generalization of de-adaptation. D). The generalization functions from Experiment 1, Experiment 2 and the control experiment. To make direct comparison, only *H2L – L2L* (learning of loading) is reported for Experiment 1 and the control experiment.

DISCUSSION

We have introduced a novel motor adaptation paradigm to perturb the hand's weight during center-out reaching. These changes in the hand's weight, similar to those encountered in everyday life, were quickly learned and generalized across reaching directions. We found a unimodal yet global generalization function for random trial-by-trial perturbations. With merely 2 training trials generalization was enhanced in all directions, peaking around the training direction. These generalization patterns were dramatically different from those previously found with previous experiments using visuomotor transformations and force perturbations with robotic manipulandums that are rarely encountered in daily life.

Task complexity/familiarity and generalization

Here we have found that the generalization functions associated with hand weight changes are much wider than those previously found with novel perturbations (e.g., Krakauer et al. 2000; Thoroughman and Shadmehr 2000). For directional generalization of learning to reach with visuomotor rotation and force fields, generalization drops to zero at about 90° or even 45° angular separations (e.g., Krakauer et al. 2000; Paz et al. 2003; Tanaka et al. 2009), while our generalization persists at the furthest angular separation of 180°. These differences suggest that, in addition to providing information about the neural representation of movement, generalization curves are also affected by the familiarity of perturbations. In this case, the familiar situation of carrying a new weight is broadly generalized to subsequent hand movements. Thus, generalization appears to have both a bottom-up component that depends on movement similarity and a top-down component that depends on the overall familiarity of the perturbation.

We interpret our results in terms of familiarity but another way of thinking about this broad generalization is in terms of a neural locus with unusually broad neuronal tuning property that specifically governs the generalization of adaptation to weight changes. Previous studies have argued that distinct areas are responsible for varying types of perturbations, such as narrowly tuned neurons in primary motor cortex corresponding to narrow generalization of visuomotor rotations (Paz et al. 2003), broadly tuned neurons in cerebellum corresponding to bimodal generalization of force-field learning (Donchin et al. 2003; Shadmehr 2004). It is thus possible to locate an area or multiple areas representing broad generalization in weight learning. However, there is currently little neurophysiological evidence for this kind of distinct circuits and it certainly invites further investigations.

From a normative perspective, the purpose of the nervous system is to allow us to successfully interact with the environment (Körding 2007). In this light, the nervous system should generalize a perturbation only if the learned dynamics are likely to be present in a new context. Besides the familiarity of the perturbation, this probability may depend on the uncertainty of our state estimation or the feedback that we receive (Wei et al. 2010), how accurately we can attribute the perturbation to internal or external sources (Berniker and Körding 2008; Wei and Kording 2009), and the typical timescales of perturbations in the world (Körding et al. 2007; Smith et al. 2006). Although it is difficult to make precise conclusions about what perturbations are “likely” without measuring natural statistics of diverse perturbations (Ingram et al. 2008), distinct generalization curves observed for visuomotor rotations, force fields, and, now, changes in hand weight are qualitatively consistent with this normative viewpoint.

Familiar perturbations might also be viewed as simple to learn. Most motor adaptation studies deliberately employed novel perturbations to induce prolonged and gradual learning. Adaptation to these perturbations are usually associated with building an internal model of the new dynamics (Shadmehr and Mussa-Ivaldi 1994). For instance, learning of a velocity-dependent force field necessitates mastery of a mapping between the position and velocity of the hand with perturbation forces (Hwang et al. 2003; Shadmehr 2004; Sing et al. 2009). Learning these novel dynamics usually require long exposure. For instance, learning visuomotor rotation needs at least 20 trials (Krakauer et al. 2000). In contrast, hand weight changes are perturbations without dependency on spatiotemporal characteristics of the movement itself and presumably can be viewed as changes of a static parameter in an internal model. As such these perturbations may be easier to learn and more readily generalized. Indeed, we found that the majority of adaptation to a weight change occurs in the first trial with near complete adaptation within 2 trials, consistent with previous findings that people can adjust finger force properly with a novel object after several attempts (Johansson and Westling 1988; Johansson 1996). Consistent with a familiarity/simplicity hypothesis, a previous study found that complex force fields, as compared to simple ones, showed much less generalization (Thoroughman and Taylor 2005). Similarly, experiments in perceptual learning also suggest that harder perceptual skills showed less generalization than easier ones (Ahissar and Hochstein 1997).

Global generalization patterns have also been found in learning of visuomotor gain, a scaling factor between hand movement amplitude and its cursor representation (Bock 1992; Krakauer et al. 2000; Pine et al. 1996; Vindras and Viviani 2002). Interestingly, this visual perturbation is also frequently present in modern daily life when we use computer mice. Thus, global generalization for visuomotor gain can also be explained by our simplicity/familiarity hypothesis. As extreme cases of unfamiliar perturbations, a recent study examined the learning of an arbitrary mapping from multi-finger movements to a cursor movement, a completely novel task where prior experience was minimally applicable (Liu et al. 2011). Not surprisingly, generalization across directions was found to be very narrow. In some sense, our perturbation and this novel perturbation sit on the two extremes of the familiarity continuum for the nervous system.

Our findings are quite different from the generalization observed in object manipulation tasks, though our weight perturbation is applied through a hand-held object. People have found that directional generalization of learning to manipulate a hammer in a virtual reality setting is rather local with a narrow Gaussian pattern (Ingram et al. 2010). We postulate that limited generalization of this familiar object is expected since representations of object dynamics are shown to be hard to generalize across orientations (Zhang et al. 2010). The other possible explanation is that the presentation of the hammer via augmented visual feedback and a robotic manipulandum prevents broad generalization across directions.

Top-down v.s. Bottom-up influence

It is quite intriguing that the global generalization features a unimodal shape as an equal generation across workspace is expected if the hand weight is a static parameter in an internal model. Single-cell recording during reaching with inertial loading showed that population activity in primate motor cortex had systematic load-dependent discharge (Kalaska et al. 1989). Interestingly, this discharge exhibited a smooth and broad tuning curve centered on the movement direction, suggesting that there exists a population of neurons modulated by both inertial load and movement direction with tuning that is consistent with the generalization curves observed here. We thus postulate that learning hand weight changes involves neuronal activity with local tuning, which leads to the unimodal pattern on top of the global generalization.

The generalization functions, discovered from psychophysical experiments on perceptual or motor tasks, have been directly linked to neuronal tuning, i.e., broader generalization relies on neurons with broader tuning (Ahissar 2001; Amirikian and Georgopulos 2000; Chou and Lisberger 2002; Tanaka et al. 2009). Specifically, narrow generalization of visuomotor rotations has been associated with narrowly tuned neurons in primary motor cortex (Paz et al. 2003), while the bimodal generalization of force-field learning has been associated with broadly tuned neurons in cerebellum (Donchin et al. 2003; Shadmehr 2004). Directional generalization patterns have also been related to the shape of learning primitives (Donchin et al. 2003; Paz et al. 2003; Thoroughman and Shadmehr 2000) and their connections (Poggio and Bizzi 2004; Tanaka et al. 2009). However, our study and some previous studies suggest that behaviorally observed generalization functions are flexible and under top-down influence. For example, although learning a single visuomotor gain generalizes globally, people can learn two conflicting gains simultaneously and effectively produce a different overall generalization function by flexibly reshaping and combining two separate functions (Pearson et al. 2010). Learning force fields with varying complexity induces distinct generalization functions where simpler force fields led to broader generalization (Thoroughman and Taylor 2005). These findings speak to the modifiability of generalization given specific task demands. Our study reveals that generalization can be changed swiftly in a few trials -- unimodal generalization increases and becomes more specific from one-trial to multiple-trial learning. This is a direct and strong support for rapid reshaping of generalization functions, simply by varying durations of exposure to the *same* perturbation. Taken together, our results suggest that top-down effects clearly influence the exact shape of the generalization function. We thus propose that the approach of simply mapping the generalization function in behavior to neuronal tuning in various areas of the brain should be taken with caution.

Block-based v.s. trial-by-trial generalization

There have not been any previous experimental attempts to compare trial-by-trial generalization side-by-side with block-based generalization. However, piecing together evidence from separate studies, we find that generalization patterns from these two learning protocols vary greatly depending on the nature of the perturbation. For visuomotor rotation, both types of learning induced narrow uni-modal generalization functions whose widths were indistinguishable (Krakauer et al. 2000; Tanaka et al. 2009). For force field learning, trial-by-trial adaptation exhibits a broader bimodal generalization function than block-based learning does (Donchin et al. 2003; Mattar and Ostry 2007; Thoroughman and Shadmehr 2000). Our study instead finds that the global generalization is enhanced from trial-by-trial learning to block learning, especially in the proximity of the training direction. For the naturalistic perturbations used here this enhancement saturated within two trials.

The enhanced generalization is consistent with the normative idea that repetitive exposure to the same weight reduces the participant's uncertainty about hand weight. In other words, the internal model of the hand weight is better formed and more readily to generalize to other directions after more exposure to the perturbation. If this is the case, why do visuomotor rotation and force field learning not show enhanced generalization with repeated exposure to the same perturbation? Here we would argue, again, that this is due to the top-down influence in motor generalization. As these are novel perturbations produced by virtual reality and robotic manipulandums, the nervous system tends to view them as local or external perturbations (Berniker and Körding 2008). The more the nervous system learns about the exact dynamics of the perturbation, the more it is "aware" of its locality and the less it will generalize to other directions. Indeed, it has been found that the population activity in motor cortex exhibits a gradual sharpening of the tuning curve during learning of a visuomotor rotation (Paz et al. 2003), suggesting the neuronal representation of the learned perturbation became more specific. This hypothesis also predicts that learning in multiple directions should induce broader generalization as the nervous system can extrapolate that perturbations are effective across directions, consistent with a previous finding that the generalization function is broadened with training in more directions (Krakauer et al. 2000). In sum, the difference between trial-by-trial and block-based generalization depends on the nature of the perturbation and it reflects the fact that generalization is under top-down influence.

It is noteworthy to mention that our enhanced generalization in block-based paradigm might be partially explained by use-dependent plasticity. Motor adaptation studies have found that repetition of movement can contribute to learning and bias subsequent movements in the direction of the perturbation (Diedrichsen et al. 2010; Huang et al. 2011). This use-dependent learning can at least contribute to the enhanced learning in the training directions, which has been observed in our generalization function. However, we also observed enhanced generalization in movement directions other than the training directions with training repetitions. Generalization of use-dependent learning has also been observed in Huang et al.'s study where repetition of reaching movements in the to-be-learned directions during visuomotor rotation adaptation can "attract" the subsequent movements when participants reach to untrained directions. Hence, this bias is a sign of use-dependent learning in the form of generalization. However, we note that in this study the manipulation of repetition and its effect share the same variable: the learning (use) in this study is about movement direction while the use-dependent generalization is also quantified as shifts in direction. Our study, instead, separates these two variables: the use is about weight perturbations and the generalization is assessed across the horizontal directions. Thus our results might serve as a strong support for the effect of use-dependent plasticity on motor generalization. Recent advances in motor learning have started to examine separate contributions from error-based learning, use-dependent learning and operant reinforcement (Huang et al. 2011). It remains an open question how different types of learning, especially use-dependent learning, contribute to the behaviorally observed generalization.

Concluding remarks

In the present study, we discovered a unique generalization pattern associated with hand weight changes and propose that motor generalization involves top-down influence where prior experience with a perturbation plays a critical role. This view complements the much-emphasized role of bottom-up learning where flexible combination of motor primitives essentially determines motor learning and generalization (Poggio and Bizzi 2004). The necessity of combing top-down and bottom-up phenomena suggests that a simple mapping between behaviorally-observed generalization functions and neuronal activity in isolated brain areas cannot provide a full account of motor generalization. In addition, our findings suggest that insights from studying motor generalization of novel perturbations should be interpreted with caution, since they may not necessarily be applicable to more naturalistic types of perturbations. Lastly, our novel experimental paradigm may provide a useful tool for neurophysiologists to study the neural substrate underlying motor learning and generalization during naturalistic perturbations.

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Author contributions:

K.W., K.K., and I.H.S conceived and designed the study; X.Y., Q.W., K.W., and Z.L. performed the experiment; X.Y. and K.W. analyzed the data; K.W., K.K., X.Y., and I.H.S prepared the manuscript.

Reference

Ahissar M. Perceptual training: a tool for both modifying the brain and exploring it. *Proceedings of the National Academy of Sciences* 98: 11842, 2001.

Ahissar M, and Hochstein S. Task difficulty and the specificity of perceptual learning. *Nature* 387: 401-406, 1997.

Amirikian B, and Georgopulos AP. Directional tuning profiles of motor cortical cells. *Neuroscience Research* 36: 73-79, 2000.

Berniker M, and Körding K. Estimating the sources of motor errors for adaptation and generalization. *Nature Neuroscience* 11: 1454-1461, 2008.

Bock O. Adaptation of aimed arm movements to sensorimotor discordance: evidence for direction-independent gain control. *Behavioural brain research* 51: 41-50, 1992.

Chou I, and Lisberger S. Spatial generalization of learning in smooth pursuit eye movements: implications for the coordinate frame and sites of learning. *The Journal of Neuroscience* 22: 4728, 2002.

Diedrichsen J, Hashambhoy Y, Rane T, and Shadmehr R. Neural correlates of reach errors. *Journal of Neuroscience* 25: 9919-9931, 2005.

Diedrichsen J, White O, Newman D, and Lally N. Use-dependent and error-based learning of motor behaviors. *The Journal of Neuroscience* 30: 5159-5166, 2010.

Donchin O, Francis JT, and Shadmehr R. Quantifying Generalization from Trial-by-Trial Behavior of Adaptive Systems that Learn with Basis Functions: Theory and Experiments in Human Motor Control. *Journal of Neuroscience* 23: 9032-9045, 2003.

Flanagan JR, and Lolley S. The inertial anisotropy of the arm is accurately predicted during movement planning. *The Journal of Neuroscience* 21: 1361, 2001.

Ghahramani Z, Wolpert DM, and Jordan MI. Generalization to local remappings of the visuomotor coordinate transformation. *The Journal of Neuroscience* 16: 7085, 1996.

Gordon J, Ghilardi MF, Cooper SE, and Ghez C. Accuracy of planar reaching movements. *Experimental Brain Research* 99: 112-130, 1994.

Huang VS, Haith A, Mazzoni P, and Krakauer JW. Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron* 70: 787, 2011.

Hwang EJ, Donchin O, Smith MA, and Shadmehr R. A gain-field encoding of limb position and velocity in the internal model of arm dynamics. *PLoS Biol* 1: E25, 2003.

Imamizu H, Uno Y, and Kawato M. Internal representations of the motor apparatus: Implications from generalization in visuomotor learning. *Journal of Experimental Psychology: Human Perception and Performance* 21: 1174, 1995.

Ingram JN, Howard IS, Flanagan JR, and Wolpert DM. Multiple grasp-specific representations of tool dynamics mediate skillful manipulation. *Current Biology* 20: 618-623, 2010.

Ingram JN, Körding KP, Howard IS, and Wolpert DM. The statistics of natural hand movements. *Experimental Brain Research* 188: 223-236, 2008.

Inoue K, Kawashima R, Satoh K, Kinomura S, Goto R, Sugiura M, Ito M, and Fukuda H. Activity in the parietal area during visuomotor learning with optical rotation. *Neuroreport* 8: 3979, 1997.

Johansson R, and Westling G. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research* 71: 59-71, 1988.

Johansson RS. Sensory control of dexterous manipulation in humans. *Hand and brain: The neurophysiology and psychology of hand movements* 381¨C414, 1996.

Körding K. Decision theory: what "should" the nervous system do? *Science* 318: 606-610, 2007.

Körding K, Tenenbaum J, and Shadmehr R. The dynamics of memory as a consequence of optimal adaptation to a changing body. *Nature Neuroscience* 10: 779-786, 2007.

Kalaska JF, Cohen D, Hyde ML, and Prud'Homme M. A comparison of movement direction-related versus load direction-related activity in primate motor cortex, using a two-dimensional reaching task. *The Journal of Neuroscience* 9: 2080, 1989.

Krakauer JW, Ghilardi MF, Mentis M, Barnes A, Veytsman M, Eidelberg D, and Ghez C. Differential cortical and subcortical activations in learning rotations and gains for reaching: a PET study. *Journal of Neurophysiology* 91: 924, 2004.

Krakauer JW, Pine ZM, Ghilardi MF, and Ghez C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J Neurosci* 20: 8916-8924., 2000.

Liu X, Mosier KM, Mussa-Ivaldi FA, Casadio M, and Scheidt RA. Reorganization of finger coordination patterns during adaptation to rotation and scaling of a newly learned sensorimotor transformation. *Journal of Neurophysiology* 105: 454, 2011.

Mamassian P, and Goutcher R. Prior knowledge on the illumination position. *Cognition* 81: B1-B9, 2001.

Mattar AAG, and Ostry DJ. Modifiability of generalization in dynamics learning. *Journal of Neurophysiology* 98: 3321, 2007.

Mussa-Ivaldi FA, Hogan N, and Bizzi E. Neural, mechanical, and geometric factors subserving arm posture in humans. *The Journal of Neuroscience* 5: 2732, 1985.

Paz R, Boraud T, Natan C, Bergman H, and Vaadia E. Preparatory activity in motor cortex reflects learning of local visuomotor skills. *NATURE NEUROSCIENCE* 6: 882-890, 2003.

Pearson TS, Krakauer JW, and Mazzoni P. Learning not to generalize: modular adaptation of visuomotor gain. *Journal of Neurophysiology* 103: 2938, 2010.

Pine ZM, Krakauer JW, Gordon J, and Ghez C. Learning of scaling factors and reference axes for reaching movements. *NeuroReport-International Journal for Rapid Communications of Research in Neuroscience* 7: 2357-2362, 1996.

Poggio T, and Bizzi E. Generalization in vision and motor control. *Nature* 431: 768-774, 2004.

Rabe K, Livne O, Gizewski ER, Aurich V, Beck A, Timmann D, and Donchin O. Adaptation to visuomotor rotation and force field perturbation is correlated to different brain areas in patients with cerebellar degeneration. *Journal of Neurophysiology* 101: 1961, 2009.

Schwarz G. Estimating the dimension of a model. *The annals of statistics* 6: 461-464, 1978.

Shadmehr R. Generalization as a behavioral window to the neural mechanisms of learning internal models. *Human Movement Science* 23: 543-568, 2004.

Shadmehr R, and Mussa-Ivaldi FA. Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience* 14: 3208-3224, 1994.

Sing G, Joiner W, Nanayakkara T, Brayanov J, and Smith M. Primitives for motor adaptation reflect correlated neural tuning to position and velocity. *Neuron* 64: 575-589, 2009.

Smith MA, Ghazizadeh A, and Shadmehr R. Interacting adaptive processes with different timescales underlie short-term motor learning. *PLoS Biol* 4: e179, 2006.

Stocker AA, and Simoncelli EP. Noise characteristics and prior expectations in human visual speed perception. *Nat Neurosci* 9: 578-585, 2006.

Tanaka H, Sejnowski TJ, and Krakauer JW. Adaptation to visuomotor rotation through interaction between posterior parietal and motor cortical areas. *Journal of Neurophysiology* 102: 2921, 2009.

Thoroughman KA, and Shadmehr R. Learning of action through adaptive combination of motor primitives. *Nature* 407: 742-747, 2000.

Thoroughman KA, and Taylor JA. Rapid reshaping of human motor generalization. *Journal of Neuroscience* 25: 8948-6953, 2005.

Tseng Y, Diedrichsen J, Krakauer JW, Shadmehr R, and Bastian AJ. Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of Neurophysiology* 98: 54, 2007.

Vindras P, and Viviani P. Altering the visuomotor gain. *Experimental Brain Research* 147: 280-295, 2002.

Wei K, and Kording K. Relevance of error: what drives motor adaptation? *Journal of Neurophysiology* 101: 655-664, 2009.

Wei K, Stevenson I, and Körding K. The uncertainty associated with visual flow fields and their influence on postural sway: Weber's law suffices to explain the nonlinearity of vection. *Journal of Vision* 10: 2010.

Wise S, Moody S, Blomstrom K, and Mitz A. Changes in motor cortical activity during visuomotor adaptation. *Experimental Brain Research* 121: 285-299, 1998.

Zhang W, Gordon AM, Fu Q, and Santello M. Manipulation after object rotation reveals independent sensorimotor memory representations of digit positions and forces. *Journal of Neurophysiology* 103: 2953-2964, 2010.

Figure Legends

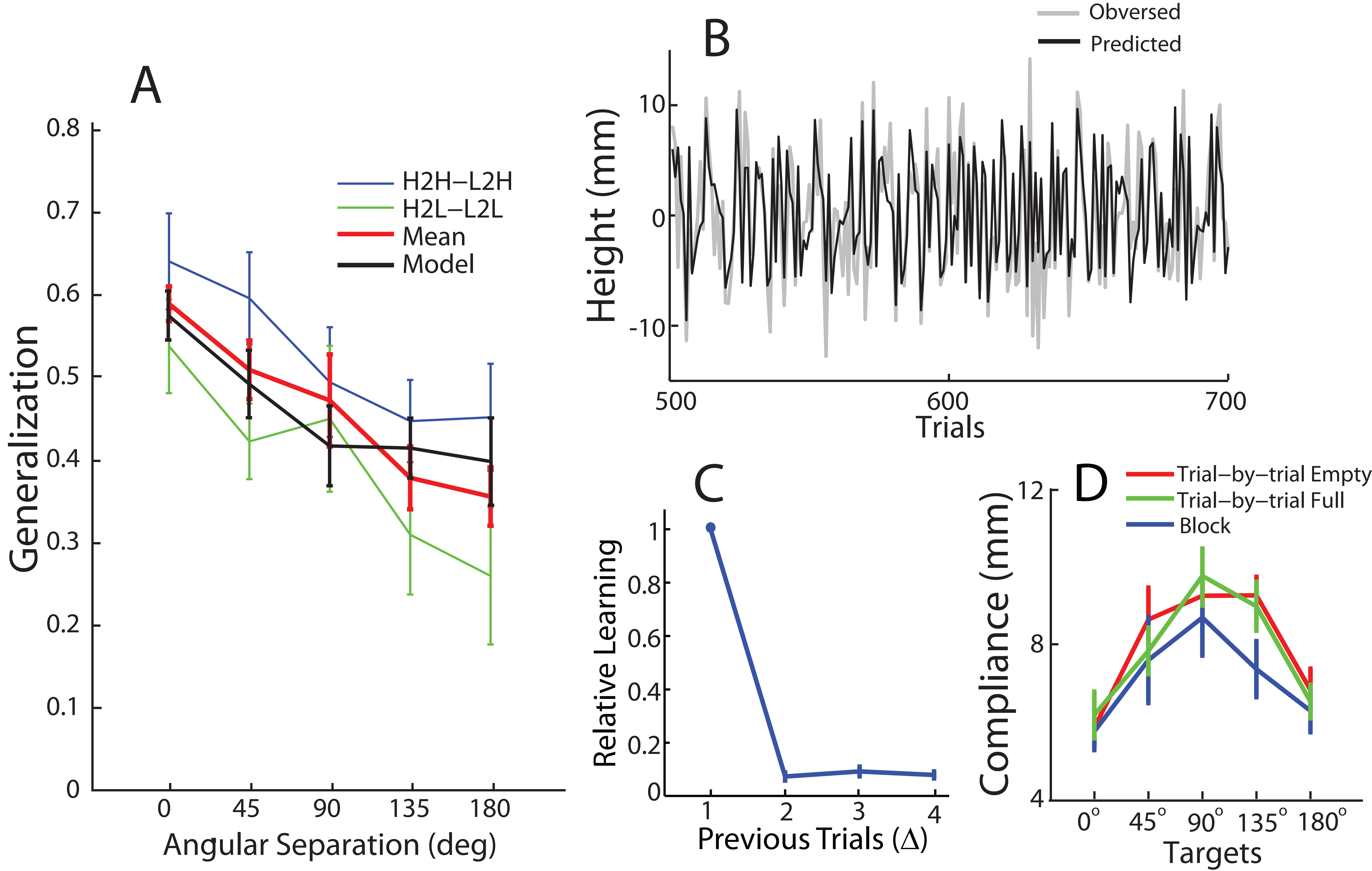
Figure 1: Experimental setup and exemplary trials. A) Experimental setup. Participants made cued, unconstrained reaches to five targets placed 15cm high, 20cm away from the starting position. Between each trial and without the participant's knowledge, the hand weight is modulated by changing a water load attached underneath the hand. Behind the participant, the experimenter can change the volume of water and, thus, weight at the participant's hand using a syringe. B) A top-down view of movement trajectories. *H2L* and *L2H* trials are plotted for a typical participant in Experiment 1. The shaded area denotes ±1 SD across trials (same below). C) Trajectory height as a function of distance from the starting position for the same participant in Experiment 1 reaching for the 90° target with 0° angular separation between trials.

Figure 2: Results from Experiment 1 with trial-by-trial hand-weight perturbations. A). Generalization functions from learning loading (*H2H* – *L2H*) and unloading (*H2L* – *L2L*), the average across both conditions, and the corresponding model-predicted generalization function. Error bars denote standard errors across participants (same below). B). Trial-by-trial changes of trajectory height for a typical participant and the corresponding model predictions. C). The relative learning (L_Δ) from previous trials as estimated from Model 2. D). Compliance of vertical hand displacement as a function of movement direction. The compliance is estimated from unexpected loading and unloading trials from Experiment 1 and 2.

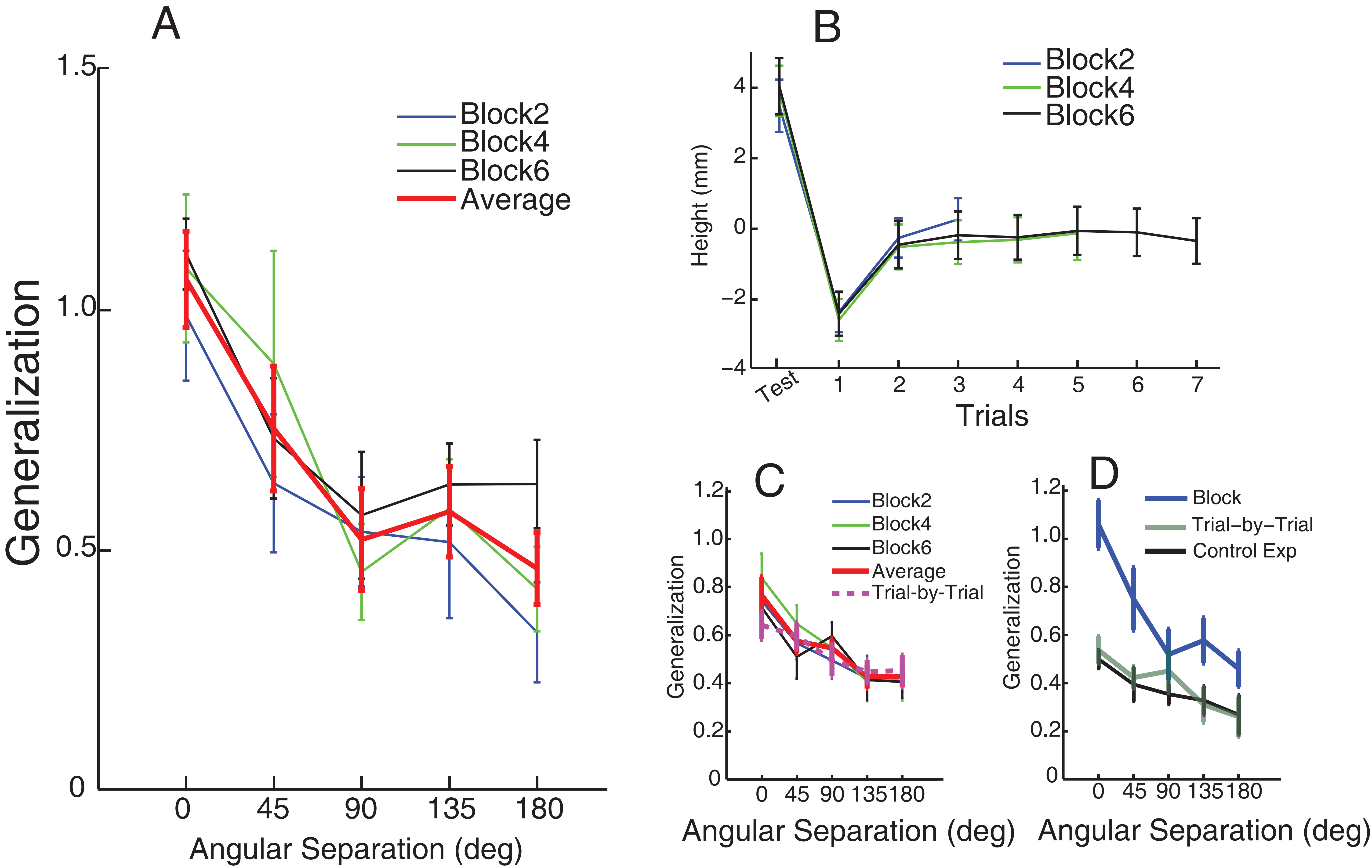
Figure 3: Results from Experiment 2 with block-based training. A). Generalization functions for unexpected unloading following training with 2 trials, 4 trials, 6 trials and their average. B).

Trajectory heights within a training block with its preceding unloading trial. Blocks with different training lengths are plotted separated. C). Similar generalization functions as in A) but associated with the loading immediately following the unloaded test trials, i.e., generalization of de-adaptation. D). The generalization functions from Experiment 1, Experiment 2 and the control experiment. To make direct comparison, only *H2L – L2L* (learning a heavy weight) is reported for Experiment 1 and the control experiment.


A
Experiment Setup
LED targets
90°
135°
180°
45°
0°
palm
brace
support
tube
syringe
B
Top-down View
H2L
L2H
200
100
0
-200
-100
0
100
200
Y Displacement (mm)
X Displacement (mm)
C
Side View
H2H
L2L
H2L
L2H
15
0
−15
0
40
80
120
160
200
Z Displacement (mm)
Distance (mm)



A
H2H−L2H
H2L−L2L
Mean
Model
Generalization
Angular Separation (deg)
0
45
90
135
180
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
B
Obversed
Predicted
Height (mm)
10
0
-10
500
600
700
Trials
C
Relative Learning
1
0.8
0.6
0.4
0.2
0
1
2
3
4
Previous Trials (Δ)
D
Trial−by−trial Empty
Trial−by−trial Full
Block
Compliance (mm)
12
8
4
0°
45°
90°
135°
180°
Targets


A
Generalization
1.5
1.0
0.5
0
Block2
Block4
Block6
Average
0
45
90
135
180
Angular Separation (deg)
B
Height (mm)
4
2
0
−2
−4
Block2
Block4
Block6
Test
1
2
3
4
5
6
7
Trials
C
Generalization
1.2
1.0
0.8
0.6
0.4
0.2
0
Block2
Block4
Block6
Average
Trial-by-Trial
0
45
90
135
180
Angular Separation (deg)
D
Generalization
1.2
1.0
0.8
0.6
0.4
0.2
0
Block
Trial−by−Trial
Control Exp
0
45
90
135
180
Angular Separation (deg)