Asymmetry in kinematic generalization between visual and passive lead-in movements are consistent with a forward model in the sensorimotor system

Abbreviated title: Spatiotemporal generalization of lead-in movements

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Abstract

In our daily life we often make complex actions comprised of linked movements, such as reaching for a cup of coffee and bringing it to our mouth to drink. Recent work has highlighted the role of such linked movements in the formation of independent motor memories, affecting the learning rate and ability to learn opposing force fields. However, while such work has described the angular generalization function representing the neural tuning of motor memory formation in state space, we have no understanding of how different movement kinematics (such as distance, speed or duration) affects the formation of these independent motor memories. Here we investigate such kinematic generalization for both passive and visual lead-in movements to probe their individual characteristics. After participants adapted to opposing force fields using training lead-in movements, the lead-in kinematics were modified on random trials to test generalization. For both visual and passive modalities, predictive compensation was sensitive to lead-in duration and peak speed, falling off away from the training condition. However, little decay was found with increasing lead-in distance. Interestingly, asymmetric transfer between lead-in movement modalities was also observed, with partial transfer from passive to visual, but very little vice versa. Overall these tuning effects were stronger for passive compared to visual lead-ins demonstrating the difference in these sensory inputs in regulating motor memories. Our results suggest these effects are a consequence of state estimation, with differences across modalities reflecting their different levels of sensory uncertainty arising as a consequence of dissimilar feedback delays.

Significance Statement

Using a force field interference paradigm, we show that the generalization of motor memory is strongly tuned to variations in lead-in kinematics, with passive lead-ins exhibiting a stronger influence and sharper tuning than visual lead-ins. This asymmetry is mirrored in the transfer of adaptation between modalities, with stronger transfer from the passive to visual condition. We suggest these differences arise due to state estimation during the lead-in, with larger delays in visual signals increasing their uncertainty. This reduces their feedback weighting compared to proprioceptive signals, producing a smaller estimated state change, and therefore smaller decay in predictive force. Overall these results provide further evidence that the human motor system uses observer-based control, based on a forward model to estimate state.

Introduction

Recent studies have highlighted key aspects for neural rehabilitation using robotic systems (Reinkensmeyer et al., 2016). However, continual progress in this area depends on understanding the mechanisms of human sensorimotor learning in order to determine the optimal presentation of sensory information to improve the rate, retention and generalization of adaptation. Although adaptation is often studied on single movements in the laboratory, we rarely

produce movements in isolation in everyday life. Rather, one movement often directly leads into another. For example, to catch a ball, we make use of visual motion information to estimate its state in order to plan and execute an interception movement. Thus, natural movements often follow directly from previous movements or from visual motion.

Recent work has shown that closely linking multiple movements together in time reduces interference in learning opposing tasks (Howard et al., 2012; 2015; Sheahan et al., 2016; Howard et al., 2017). In particular, distinct past movements act like a contextual cue, enabling adaptation to opposing viscous curl fields when these movements are preceded by unique lead-in motions, each associated with one of the dynamics (Howard et al., 2012). This shows that motor learning and recall depends not only on the current state of the arm during a movement, but also on its preceding states. Interestingly, active, passive or visual lead-in movements were all equally effective at reducing interference. This indicates that sensory feedback relating to motion is sufficient to affect adaptation, even when no active movement is involved. The contextual effect of this prior movement disappears as the time between lead-in and adaptation movements exceeds about half a second, indicating that the representation of past state decays quickly over time. This suggests a strong link between the representation of state and the theory of neural population dynamics (Churchland et al., 2012; Pandarinath et al., 2015).

Dynamic adaptation to a single force field occurs locally; after training in a specific movement, the recall of predictive compensation decays as the movement angle (Thoroughman and Shadmehr, 2000; Donchin et al., 2003; Howard and Franklin, 2015; 2016) or distance (Gandolfo et al., 1996; Goodbody and Wolpert, 1998; Mattar and Ostry, 2007) deviates from the training condition. The Gaussian-like angular generalization observed in these studies has also be found for lead-in movements, with different lead-in modalities exhibiting different characteristics, both in terms of their absolute level of influence, but also in their sharpness of tuning. In particular both active (Sarwary et al., 2015) and passive lead-in movements (Howard and Franklin, 2015) show narrower and deeper tuning than visual lead-in movements (Howard and Franklin, 2016).

Interference studies have been widely adopted to investigate contextual effects on motor learning, and to examine if contextual cues can assist in the learning of opposing dynamics (Brashers-Krug et al., 1996; Gandolfo et al., 1996; Krakauer et al., 1999; Karniel and Mussa-Ivaldi, 2002; Caithness et al., 2004; Nozaki et al., 2006; Howard et al., 2013). Such interference paradigms are more sensitive to generalization effects of contextual cues than single field paradigms, and have been used effectively to examining the angular generalization characteristics of lead-in movements (Howard and Franklin, 2015; 2016). Using these paradigms it has been possible to extract features of the neural basis functions underlying dynamical adaptation, allowing for the development of simple computational models (Howard et al., 2017). However, we still lack basic information on the generalization features of lead-in movements for different kinematics such as duration or distance.

Here, we first characterize the generalization of passive and visual lead-in movements across different kinematics using an interference paradigm. In two separate experiments, we examine generalization across distance and duration (and the dependent variable of speed) of passive and visual lead-in movements. Second, in order to gain insight into any commonality between the neural resources employed in passive and visual lead-in movements, we also investigate how adaptation transfers between these two different lead-in modalities.

Methods

Experimental Design

Subjects. Sixteen human participants were randomly allocated to two experimental groups that each performed one experiment. Eight participants (7 female, aged 24.8 ± 5.0 years, mean ± sd) performed the passive lead-in experiment. Eight further participants (6 female; aged 27.4 ± 6.7 years) participated in the visual lead-in experiment. All participants were right handed according to the Edinburgh handedness questionnaire (Oldfield, 1971), and naïve to the aims of the study. All participants provided written informed consent to the protocol before participating in the experiment, which had been approved by the University of Cambridge Ethics Committee. The methods were carried out in accordance with the approved guidelines.

Apparatus. Experiments were performed using a vBOT planar robotic manipulandum and its associated virtual reality system (Howard et al., 2009). Handle position is measured using optical encoders sampled at 1000 Hz, and motors operating under torque control allow the application of end-point forces. A force transducer (Nano 25; ATI), mounted under the handle, measures the applied forces, and its output signals were low-pass filtered at 500 Hz using analogue 4th pole Bessel filters prior to digitization. To reduce body movement participants were seated in a sturdy chair in front of the apparatus and firmly strapped against the backrest with a four-point seatbelt. During an experiment, participants grasped the robot handle in their right hand while their right forearm was supported by an air sled, constraining arm movement to the horizontal plane. Participants could not view their hand directly. Instead veridical visual feedback was used to overlay images of the starting location, via point, final target, (all 1.25 cm radius disks) and a hand cursor (0.5 cm radius red disk) using the virtual reality system. This ensured that the visual cursor appeared to the participant in the same plane and at the same location as their hand. Data was collected at 1000 Hz and logged to disk for offline analysis using Matlab (Matlab, The MathWorks Inc., Natick, MA, USA).

Force Fields. In the adaptation movement, participants performed reaching movements either in a null field condition, a velocity-dependent curl force field (Gandolfo et al., 1996), or a mechanical channel (Scheidt et al., 2000). The curl force field was implemented as:

$$\begin{bmatrix} F_x \\ F_y \end{bmatrix} = k \begin{bmatrix} 0 & -1 \\ 1 & 0 \end{bmatrix} \begin{bmatrix} \dot{x} \\ \dot{y} \end{bmatrix} \quad (1)$$

where the field constant k was set to a value of ±16 $Nm^{-1}s$, and the sign determines the direction (CW or CCW) of the force-field. Each participant experienced both force field directions. The direction of the force field was always associated with a specific direction of a prior contextual movement. The relationship between the contextual movement direction and curl field direction (CW/CCW) was counterbalanced across participants.

Condition	Duration [ms]	Distance [cm]
Passive training	700	10
Visual training	700	10
Passive/Visual test channel	700	10
Passive/Visual probe channel	1400	20
Passive/Visual probe channel	1050	15
Passive/Visual probe channel	420	6
Passive/Visual probe channel	210	3
Passive/Visual probe channel	1400	10
Passive/Visual probe channel	1050	10
Passive/Visual probe channel	420	10
Passive/Visual probe channel	350	10
Passive/Visual probe channel	700	20
Passive/Visual probe channel	700	15
Passive/Visual probe channel	700	6
Passive/Visual probe channel	700	3
Passive/Visual probe channel	1050	20
Passive/Visual probe channel	350	3

Table 1. Generalization conditions

Mechanical channel trials were implemented using a spring constant of 6,000 Nm^{-1} and a damping constant of 30 $Nm^{-1}s$ perpendicular to the direction of motion throughout the movement between the central location and the final target. Channel trials were only produced on the movements to the 0° target with corresponding lead-in movements starting at 135° or 225°.

Protocol

Two separate experiments were performed to examine the generalization of the learning associated with one contextual movement to other contextual movements with different kinematic profiles (within the same modality), as well as the transfer of learning between passive and visual lead-in conditions (across the modalities).

After an initial pre-learning session in a null field, participants were exposed to the curl force fields (learning phase). Channel trials were used to examine adaptation to the novel dynamics, in which the lead-in movement duration, speed and distance were varied. In addition, the modality of the lead-in movement was occasionally changed to examine transfer. The trial parameters for both experiments are shown in Table 1 and the kinematics of the lead-in movements can be seen in Fig 1. On these trials, the lead-in movement was chosen from one of 15 different movements with distances ranging from 3 cm to 20 cm and durations ranging between 210 ms to 1400 ms.

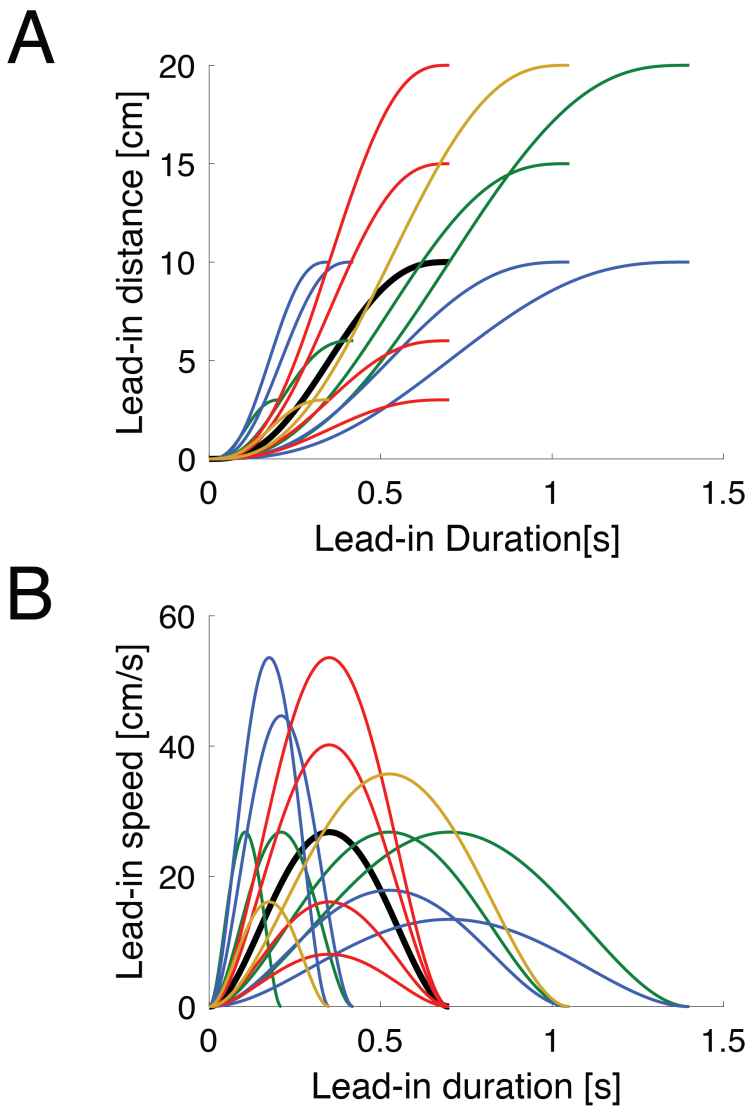

Figure 1. Kinematics of lead-in movements used for testing generalization. **A** Profiles of movement distance versus duration of lead-in probe conditions across all conditions. Thick black line indicates the training lead-in motion. Colors indicate specific conditions that are matched across duration (red), peak speed (green), or duration (blue). **B** Lead-in movement kinematics of peak speed as a function of duration.

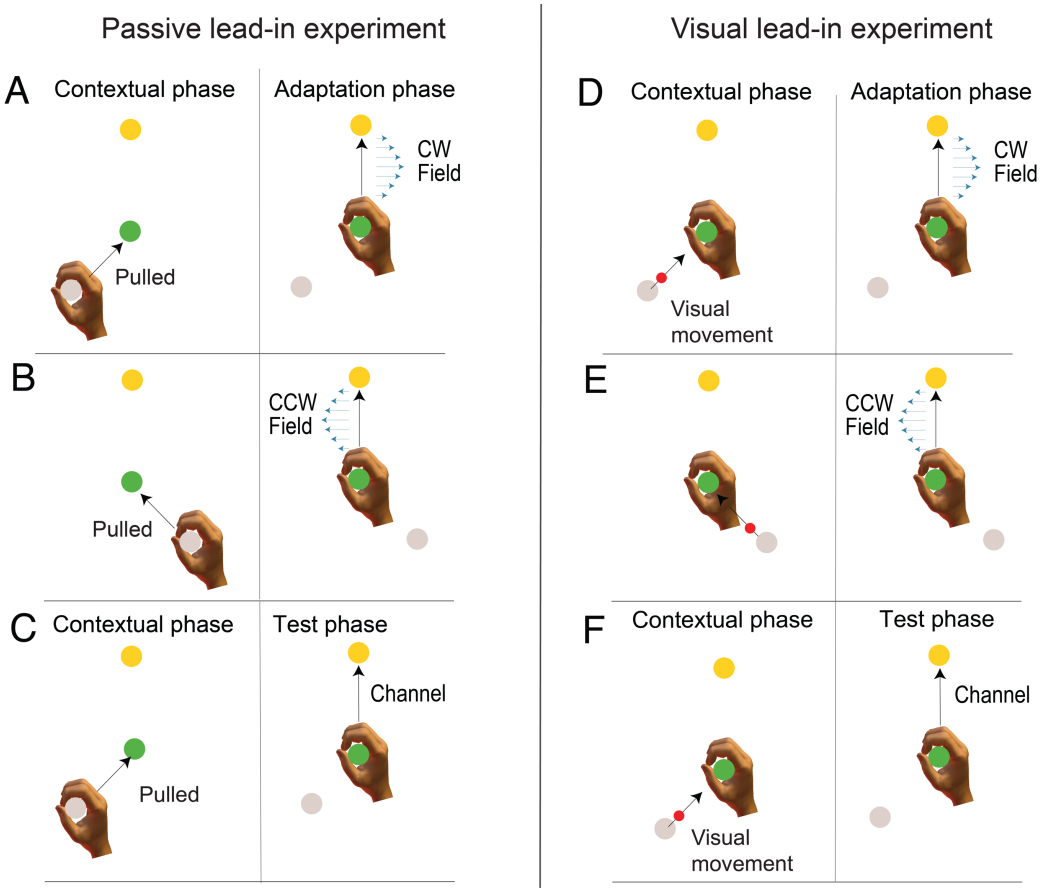

Figure 2. Experimental Design. **A-C**: Passive lead-in generalization experiment. **A** Participants first experienced an initial passive lead-in motion from a starting position (grey circle) to the central target (green circle) and then immediately made a second active movement to the target (yellow circle) on which a curl force field (blue arrows) could be applied. **B** An initial movement from a different starting target was associated with the opposite force field on the second movement. The direction of curl force field and lead-in movements were counterbalanced across participants. **C** In order to examine learning rate and generalization, random trials in which the contextual movement was followed by a mechanical channel on the second movement to the target were applied. **D-F**: Visual lead-in generalization experiment. **D** Participants initially observed an initial visual cursor movement (red circle) from the grey starting circle to the central target (green circle). Once the cursor entered the central target, participants immediately performed a second active movement to the target (yellow circle) on which a curl force field (blue arrows) could be applied. **E** An initial cursor movement from a different starting target was associated with the opposite force field on the second movement. **F** On random trials, after the visual lead-in motion, a mechanical channel was applied on the active movement to the target to measure predictive compensation.

Experiment 1. Passive lead-in movements.

All trials consisted of a two-part movement: an initial lead-in movement followed directly by an adaptation movement (Fig 2A-C). The first part was a

contextual lead-in movement from a starting location to a central via point. This contextual lead-in movement was normally 10 cm in length during all null and force field training conditions. The second part was an 18cm adaptation movement to the final target. Only during the adaptation part of the movement could participants experience a force field (or channel trial). The lead-in movement direction (+45° or -45° relative to final target direction) was indicative of the direction of the curl force field on the adaptation movement (clockwise or counterclockwise). The adaptive part of the movement was made to one of two final targets, located at 0° and 270° degrees relative to the via point. The preceding contextual movements started from one of 3 locations, namely at 135° or 225° and 45° or 135° degrees respectively, and end at a central via-point. Together this produced four possible two-part movements (combinations of lead-in and adaptation movement).

In experiment 1, the contextual lead-in movement was comprised of a passive movement of the participant's hand. This passive movement was produced by the robotic manipulandum passively moving the participant's hand while no cursor was presented. Each trial began by displaying the start location for the lead-in movement, the central location and final target. The vBOT then moved the participant's hand to the lead-in start location. Once the handle was stationary within the start location for 300 ms, a beep was generated indicating the start of the trial. At this time, the handle of the robotic system moved to the central via-point following a minimum jerk trajectory. The training contextual movement was a 10cm movement of duration 700 ms. Once the hand reached the central location, participants were required to produce an active adaptation movement from the central location to the final target location. The dwell time of the hand within the central via point was required to between 0-250 ms, otherwise a warning was provided. If dwell time exceeded 500ms then the trial was aborted and repeated. If the second movement (adaptation movement) duration was between 450 ms and 600 ms a "Great" message was displayed; otherwise an appropriate "Too Fast" or "Too Slow" warning was shown. Force fields and channel trials were only ever presented during this second movement.

As many trials were required, each experiment was performed in two separate sessions on different days. There were 1546 and 1580 trials on days 1 and 2 respectively, providing a total of 3126 trials. Participants were required to take short rest breaks approximately every 200 trials (195-205 trials) but could rest at any time between trials. The trials were organized as follows:

Day 1

Pre-exposure: The pre-exposure phase started with 2 blocks of 40 trials. A block consisted of 36 Null trials and 4 channel trials (Total 80 trials: 72 null trials, 8 training condition channel trials). Next, participants were provided with three repetitions of each of the 34 generalization channel trials (Total 102 generalization condition channel trials) to ensure they had prior experience of the generalization trial conditions. Finally, 2 blocks of null field trials (36 null trials and 4 channel trial) were performed.

Exposure Training: During the exposure phase, the participants were exposed to the curl force fields during the adaptation movement. This phase consisted of 12 blocks of 40 trials (Total 480 trials: 432 field trials, 48 training condition channel trials).

Generalization Testing: This examined generalization of the learned predictive compensation by pseudo-randomly interspersing trials with curl field exposure with trials in which channel trials were preceded by the full range of contextual movements (different durations and distances). This consisted of 6 blocks of 134 trials, which meant that there were 6 repetitions of each of the 34 generalization channel trials. (Total 804 trials: 600 field trials, 204 generalization condition channel trials). Generalization conditions are graphically illustrated in Fig. 1.

Day 2

Exposure Training: In the second session, training was briefly resumed. The phase consisted of 6 blocks of 40 trial blocks (Total 240 trials: 216 field trials, 24 training condition channel trials).

Generalization Testing: Similar to the session of Day 1, participants performed 10 blocks of 134 trials, providing 10 repetitions of each of the 34 generalization channel trials. (Total 1340 trials: 1000 field trials, 340 generalization condition channel trials).

Generalization lead-in conditions, which were always followed by a channel trial on the adaptation movement, were chosen to sample lead-in distances between 3 - 20 cm, peak speeds between 8.04 - 53.57 cms^{-1} and durations between 210 – 1400 ms. In addition, a transfer condition was included in which the lead-in motion was occasionally substituted by a visual moving cursor and a reversed direction visual cursor.

Experiment 2. Visual lead-in movements.

Experiment 2 was had a similar design to Experiment 1, except that the contextual lead-in movements for both training and testing consisted of a visual movement of the cursor (Fig 2D-F). The training contextual lead-in movement again followed a minimum jerk trajectory of duration 700 ms from the start to the central location. During this time, the participant's hand remained stationary at the central location. Immediately after the cursor reached the central location, the participant made an active reaching adaptation movement from the central location to the final target. The same variations of generalization movement trials were performed (but with visual instead of passive motion). In addition, a transfer condition was used in which a passive movement lead-in was performed. Again, a reversed visual cursor condition was also employed.

Data Analysis

The experimental data was analyzed offline using Matlab R14. Statistics to examine differences between the generalization from visual lead-in and passive lead-in movements were performed in JASP 0.9.2 (JASP Team, 2018) using both the ANOVA and Bayesian ANOVA. To examine learning, kinematic error on the adaptation movements and force compensation on the channel trials were used.

Kinematic error. For each null and curl field trial, the kinematic error was calculated on the adaptation portion of the movement. This was quantified as the maximum perpendicular error (MPE), which is the maximum deviation of the hand path to the straight line joining the movement starting location to the target. For each participant, the average MPE over 8 trials was calculated. The sign of the MPE was flipped appropriately so that results from CW and CCW field trials could be appropriately combined together in this calculation. The mean and standard error (SE) of MPE was then computed across all participants.

Force compensation. On each channel trial, force exerted by participants perpendicularly into the wall of the simulated channel was measured to estimate predictive feedforward adaptation. This method is preferable to relying on a reduction in kinematic error during force field learning, which can also arise from muscle co-contraction (Burdet et al., 2001; Franklin et al., 2003; Milner and Franklin, 2005). The measured channel force was regressed with the velocity of movement along the channel during the same period and then scaled by the field strength. This yielded an estimate of the level of force compensation present on the given channel trial (Smith et al., 2006). For plotting purposes, the force compensation data was averaged across 2 channel trials for each participant. The mean and standard error (SE) of compensation was then computed across all participants to examine the generalization functions.

Results

In the passive lead-in experiment, participants performed active reaching movements to a target after being passively moved from a start position to a central target. After initial movements in a null field, participants were presented with a curl force field during the active movement. The direction of the curl field depended on the angle between the passive movement and active movement (Fig 2A,B). When presented with the curl force field, participants' adaptation movements were disturbed, producing large errors that were gradually reduced over the exposure phase (Fig 3A). Throughout the experiment channel trials were introduced on random trials in order to measure the predictive force compensation throughout adaptation (Fig 2C). Over a similar timescale as the reduction in kinematic error, force compensation increased, reaching just over 63% compensation averaged over both force fields (Fig 3B). A small decay in the force compensation and increase in the kinematic error can be seen between day 1 and the start of day 2.

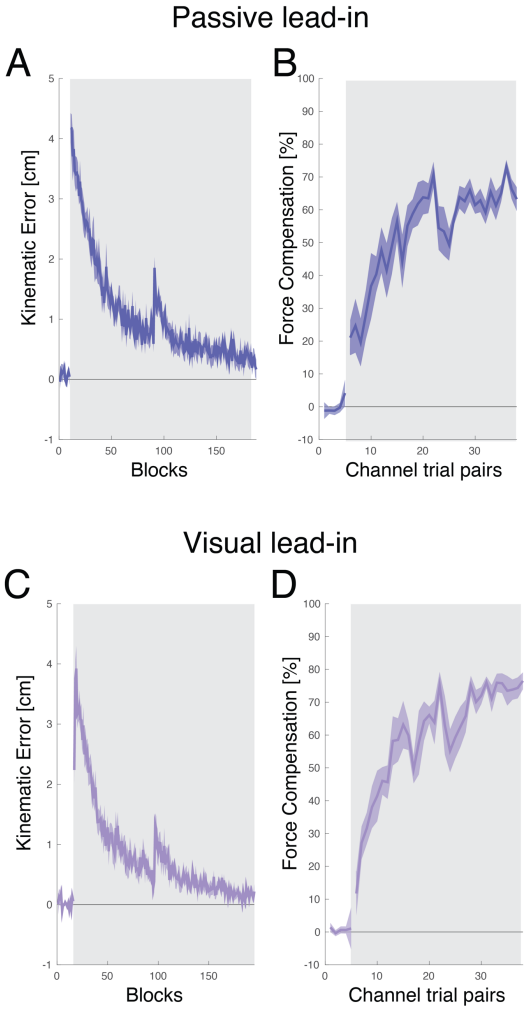

Figure 3. Adaptation to two opposing force fields. **A** Mean and SE of MPE across over 8 participants for the passive lead-in experiment as a function of blocks of 8 trials. **B** Mean and SE of percentage force compensation for pairs of channel trials (one for each force field direction) throughout the passive lead-in experiment where the lead-in movement was the same as the training trials. **C** Mean and SE of MPE for the visual lead-in experiment. **E** Mean and SE of percentage force compensation for the visual lead-in experiment.

Participants in the visual lead-in experiment performed a similar protocol but where the lead-in movements were purely visual in nature (Fig 2D-F). Again, when presented with the curl force field, participants' adaptation movements were disturbed, producing large errors that were gradually reduced over the exposure phase (Fig 3C). Over a similar timescale, force compensation increased, reaching approximately 70% compensation averaged over both force fields (Fig 3D).

On random trials late in the adaptation phase, channel trials were applied with a range of different lead-in movement kinematics (Fig 1) in order to examine generalization. After learning the force fields with the passive lead-in movement, variations in the kinematics of this lead-in movement produced a range of generalization levels (Fig 4A). As the testing lead-in movements

varied further away from the training kinematics the predictive force level decreased. A similar finding is shown for the generalization after learning a visual lead-in movement (Fig 4B). However, in this condition only small decreases in the predictive force is seen over a wide range of changes in the lead-in kinematics.

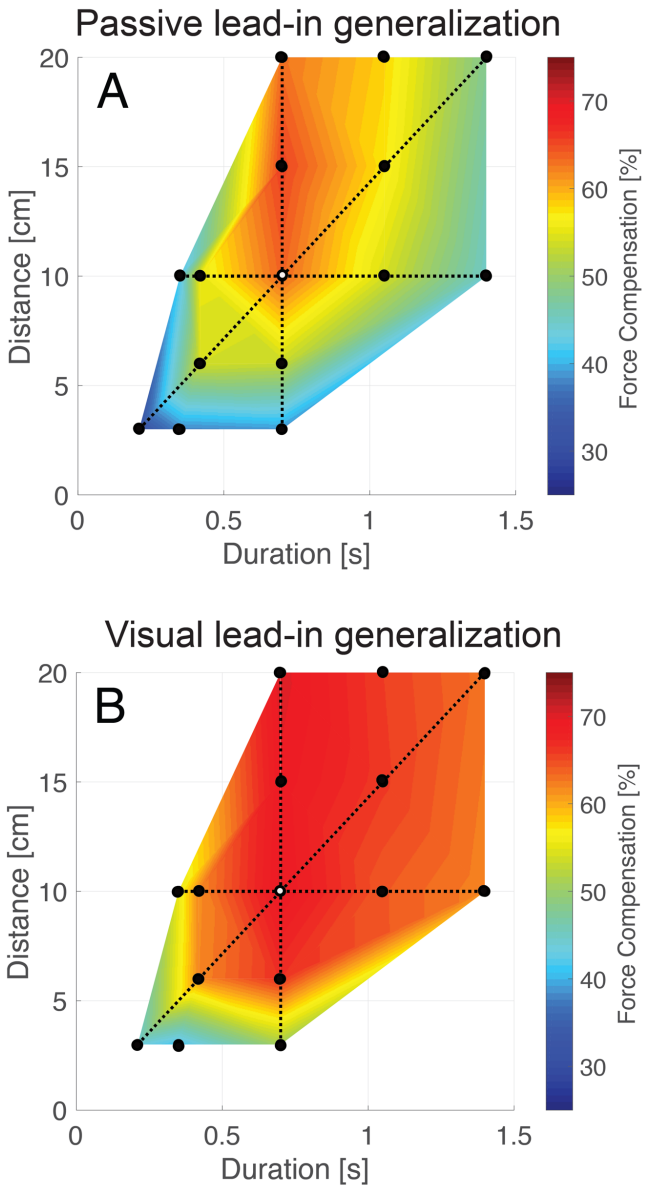

Figure 4. Generalization surface plots for passive and visual lead-in movements. **A** Surface plot of generalization for passive lead-in movements. The percentage force compensation is represented by color and plotted against lead-in duration and lead-in distance. The black circle with a white center indicates the result at the training condition. The solid black dots indicate points for which measurements were made on probe trials. The black dotted lines correspond to conditions with the same training lead-in distance of 10cm, same training lead-in duration of 0.7s or same training lead-in speed of 26.7cm/s. The legend shows the correspondence between color and percentage perfect force compensation. **B** Surface plot of generalization for the visual lead-in condition.

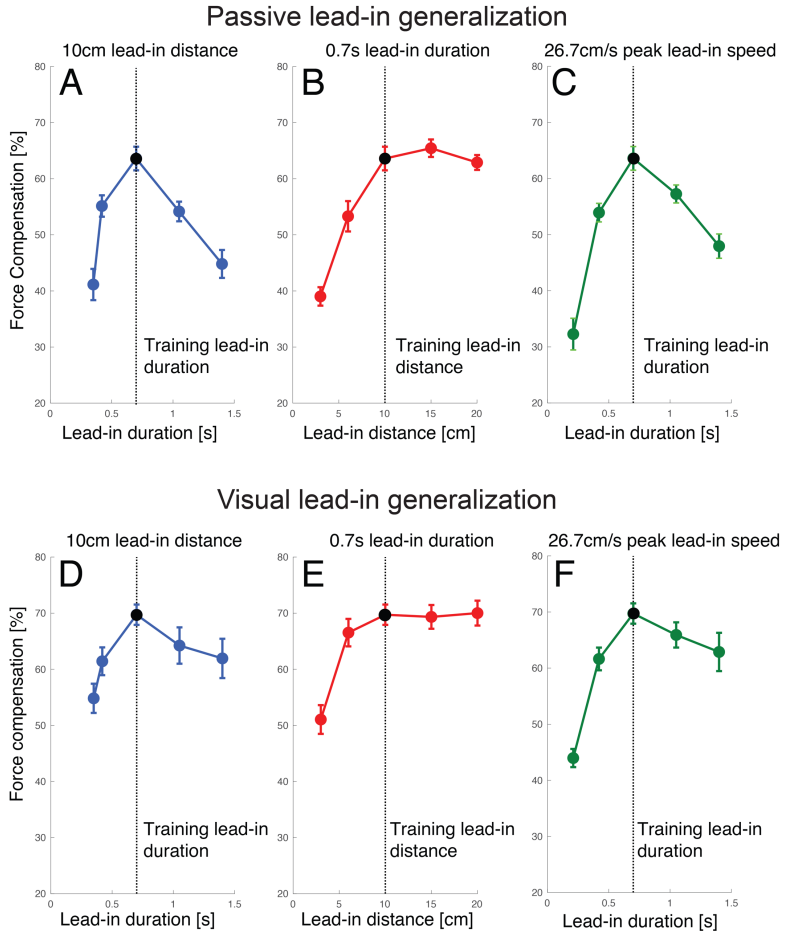

Figure 5. Generalizations results for both passive and visual lead-in conditions plotted for fixed values of lead-in distance, lead-in duration and lead-in speed. **A-C** Results of passive lead-in experiments. The dotted lines indicate the training values of lead-in distance and lead-in duration. Error bars indicate standard error of the mean. **A** Effect of changing lead-in duration for fixed 10cm lead-in distance. In this panel, lead-in distance is held constant and the movement duration (shown on the x-axis) and speed vary. **B** Effect of changing lead-in distance (and peak speed) across conditions with a fixed 700ms lead-in duration. **C** Effect of changing lead-in duration (and distance) across conditions with a fixed 26.7cm/s lead-in speed. **D-F** Corresponding results for visual lead-in condition.

Across the different lead-in movement kinematics, several conditions had the same duration, peak velocity or distance as the learned training condition (dotted lines in Fig 4). Here we examine the predictive force compensation values over these conditions in more detail (Fig 5). The results for the passive lead-in condition show strong variations over changes in all three parameters (Fig 5A-C). In panel A, lead-in distance is held constant and the movement duration (shown on the x-axis) and speed vary. In panel B, lead-in duration is held constant and the movement distance (shown on the x-axis) and speed vary. In panel C, lead-in speed is held constant and the movement duration (shown on the x-axis) and the distance vary. The dotted lines indicate the training values of lead-in distance and lead-in duration. It can be seen that the recall of predictive compensation was strongly affected by changes in the

duration of the movement (shown for constant distance conditions in Fig 5A and constant speed conditions on Fig 5C). There was a strong tuning effect centered around the movement duration used for training, with compensation falling off as movement duration either increased or decreased from that value. However, changing lead-in distance produced different effects. While reducing lead-in distance again reduced compensation, increasing movement distance from the training value had little effect (Fig 5B).

In the visual lead-in condition, we found slightly less pronounced decay as the some of the kinematics were varied while others remained constant (Fig 5 D-F). Again, it can be seen that compensation was affected by changes in the duration of the movement. Although there was a tuning effect centered around the movement duration using for training, the fall off as duration deviated from the training value was less than in the passive lead-in condition (Fig 5D). As the training distance varied but duration was fixed, we saw the least decay, especially for longer distances (Fig 5E). Finally, as the peak speed was fixed, we found small decay the other variables were changed. (Fig 5F).

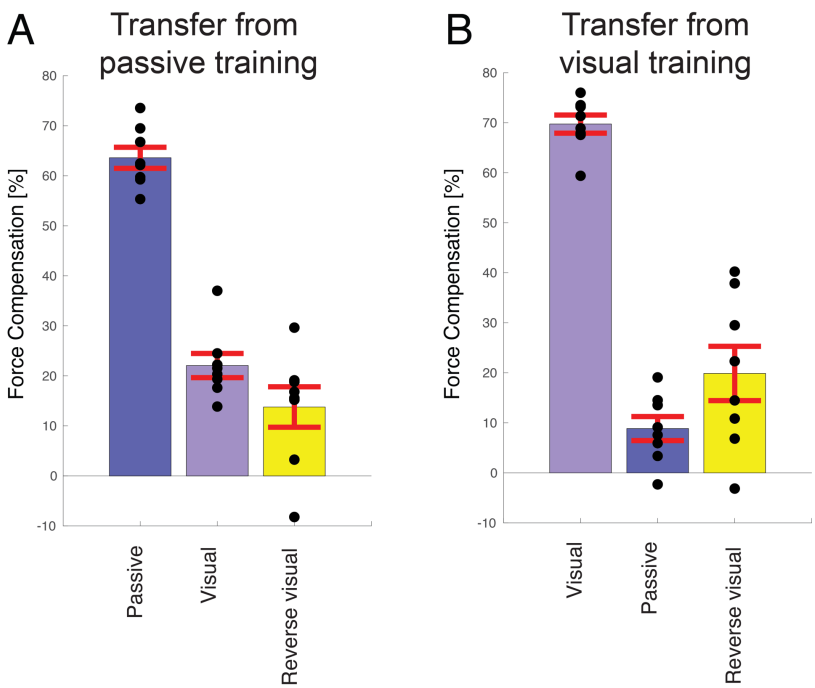

Figure 6. Comparison of transfer across sensory modality or to reversed visual cursor. **A** Transfer from passive lead-in to visual lead-in or reversed visual lead-in. For comparison the learned force compensation on passive movements is shown. Black circles indicate the results of individual participants. Error bars indicate standard error of the mean. **B** Transfer from visual lead-in to passive lead-in or reversed visual lead-in.

If we compare the generalization of the predictive compensation across the two experiments, we can see one major finding; namely that the overall tuning effects were much more pronounced for the passive lead-in condition compared to the visual lead-in condition. Visual lead-in generalization showed much less sensitivity to variations in lead-in kinematics. Indeed, whereas passive lead-ins resulted in a 2D monotonic curved surface in the dimensions

of duration and distance (Fig. 4A), the corresponding surface for visual lead-ins (Fig. 4B) exhibits a large region consisting of a flat planar surface. To test if this difference in the generalization across kinematics between passive and visual lead-in movements is statistically significant, we performed ANOVAs on the force compensation results (with main effects of kinematic condition (14 levels) and lead-in modality (2 levels: visual or passive)). To do so, the force compensation for each testing condition was normalized with respect to the value at the trained condition for each participant. We found strong differences between the generalization results of the visual and passive lead-in movements (lead-in modality) using both frequentist ($F_{1,196}$=32.477; $p<0.001$) and Bayesian (BF=13.664) ANOVAs. This highlights a clear difference between visual inputs and passive inputs as a contextual signal for motor adaptation, extending our previous findings (Howard and Franklin, 2015; 2016).

We also investigated how learning opposing force fields with contextual cues in one sensory modality would transfer to the other sensory modality. To investigate this, occasional channel trials were used with a lead-in in the other modality. It can be seen that there is asymmetric transfer between passive lead-in and visual lead-in movements (Fig 6). Although there was partial transfer from passive to visual lead-in movements (Fig 6A) with values reaching just above 20%, there was much less transfer from visual to passive lead-in movements (Fig 6B) with values just under 10%. To compare the level of transfer between the two modalities, the transferred adaptation was scaled according to the final level of adaptation in each experiment. The transfer from passive to visual was significantly larger than the transfer from visual to passive ($F_{1,14}$=15.9, $p<0.001$; BF=23.2). Thus, there is a clear asymmetry between the transfer of adaptation between these two sensory modalities.

Finally, we examined how learning the visual lead-in movement would transfer to a completely reversed visual cursor (with the same duration and distance). To balance conditions and the number of trials across experiments, this was also tested for the passive lead-in. As expected, there was little transfer from passive lead-in to reverse visual lead-ins, although this value was only about 75% of the forward visual lead-in transfer. The transfer from the visual training to the reversed visual lead-in was also low (approximately 20%) showing that the predictive compensation is sensitive to the direction of the visual motion. The recall of compensation in the reversed cursor transfer conditions were quite variable, as indicated by the spread of data points (black dots) shown as the mean of each individual participant.

Discussion

We investigated the kinematic generalization characteristics of passive and visual lead-in movements using a force field interference paradigm. Participants first experienced a lead-in movement and then immediately made an active movement in a curl force field where the field direction was associated with the lead-in movement. Channel trials within the active movement examined how predictive compensation varied as lead-in

kinematics were varied. In the first experiment lead-in movements were passive, whereas in the second experiment they were visual. For both modalities, recall of predictive compensation decreased as the duration of the lead-in movements deviated from the training condition. Reducing lead-in distance also reduced compensation but increasing lead-in distance had little effect on the force generalization. Our results show that although passive and visual lead-in movements influence memory formation and recall in subsequent movement, passive motion exhibits narrower generalization characteristics, whereas visual motion is much less sensitive to kinematic change.

These generalization results further characterize the neural tuning exhibited by lead-in movements, extending beyond the directional tuning seen previously. The observation that passive lead-ins were more sensitive to changes in kinematics than visual lead-ins is consistent with the prior observations examining angular generalization (Howard and Franklin, 2015; Sarwary et al., 2015; Howard and Franklin, 2016). Namely that active and passive tuning was more pronounced and narrower than the wider tuning seen in the visual condition. More recently it was shown that the tuning characteristics of different lead-in modalities could explain why angular variability of active lead-in movements affects the learning rate in two-part movement tasks, whereas no such effect exists for visual lead-in movements (Howard et al., 2017). Our current results suggest that variations in the speed or duration of lead-in movements could provide similar decrements in learning rate, whereas an increase in movement distance would not have much effect. This might have important implications for rehabilitation, suggesting learning and recovery would be faster for training routines with consistent lead-in kinematics. One caveat is that such routines might also produce less generalization across tasks, as the adaptation is more likely to be learned specifically for the trained lead-in movement.

In both experiments, to examine transfer of adaptation across modality, a visual lead-in cursor motion occasionally replaced the passive lead-in, and vice versa. Interestingly, there was an asymmetric transfer between passive and visual lead-in movements, with partial transfer from passive lead-in movements to visual lead-in movements, but almost no transfer from visual to passive lead-in movements. Transfer could arise because passive lead-in movement partially engages neural mechanisms shared by the visual observation of movement, but not the converse. This result may be due to asymmetry in the connections between the neural substrates. Alternatively, it could arise because the visual feedback pathway has a lower gain due to the uncertainly introduced by the longer time delay associated with visual information (Crevecoeur et al., 2016). The current observation that passive lead-in are more strongly tuned in duration than visual lead-ins, as well as the former results that the absolute level of influence of passive lead-ins (Howard and Franklin, 2015) is higher than for visual lead-in (Howard and Franklin, 2016) supports the latter hypothesis.

The wide ranging results from studies examining contextual cues for learning opposing dynamics have demonstrated that not all sensory signals are able to

influence motor learning (Hwang et al., 2003a; 2003b; Wainscott, 2004; Cothros et al., 2009; Addou et al., 2011; Yokoi et al., 2011; Hirashima and Nozaki, 2012; Howard et al., 2013; Sarwary et al., 2015; Nozaki et al., 2016). For example, color has essentially no effect (Howard et al., 2013). In addition to the strong effects of prior movements, it has been shown that particularly effective contextual cues relate to state; for example limb state and physical locations (Hwang and Shadmehr, 2005; Yeo et al., 2015), or different visual locations of the cursor and targets (Hirashima and Nozaki, 2012). Indeed, a location cue could constitute a complete physical shift of the movement task, or just a shift of one of its two essential components; namely a change in the location of the visual feedback, or a change in the physical location of the task with identical visual feedback. Further experiments have shown that future state also effects motor learning in an analogous way (Howard et al., 2015), with this effect depending on movement planning rather than execution (Sheahan et al., 2016).

On the face of it, it appears that there are multiple types of contextual cues that strongly influence motor memory formation. Here we propose that a factor they all have in common is that they are related to either past, current, or future state of the limb; or are signals used in the estimation of such limb states. That is, setting up the sensorimotor system in a different state before (or at the end of) a movement allows the formation and recall of different motor memories. This suggests that some contextual cues (such as visual lead-in movement or location in the visual workspace) are simply effective because the motor system makes use of these signals within a state estimation mechanism to determine the state of the arm. Such state estimation can only be made on the basis of sensory feedback and efference copy. This hypothesis would be consistent with the observation that visual or proprioceptive movements are as effective an active movement. It would also explain why a visual change of state can be as effective as a complete change in the physical state of the limb. Moreover, it can explain why vestibular inputs could also be used to learn opposing dynamics (Sarwary et al., 2015) but why color cues have much less effect on the adaptation system (Howard et al., 2013).

In order to reach with our arm to a specific location, our sensorimotor control system needs to know the initial limb state, and then activate the appropriate muscles in a specific pattern to generate forces that bring the arm into the final state to meet the task requirements. To make this movement robust in the face of noise and disturbances, this process does not simply rely on feedforward control, but makes use of sensory feedback of our arm's state, enabling online correction in any task-relevant deviation from the goal of our movement. Arm state can be estimated through the combination of appropriate sensory feedback signals such as proprioception from the skin muscles and joints, visual information, and vestibular inputs. However due to neural signal transmission and processing delays, motor responses to proprioceptive and visual feedback only start producing force after delays of 50 ms and 140 ms respectively. Such delays represent a challenge in the design of a feedback control systems, since using direct feedback from delayed signals can lead to instability.

To deal with delay, Smith proposed an architecture which involves using immediate feedback from the output of a forward model of the plant, (known as an observer), rather than from the plant output directly (Smith, 1959). Miall and Wolpert suggested that the Smith predictor architecture could account for delays in the human motor system (Miall et al., 1993; Miall and Wolpert, 1996). This approach is also often use engineering applications, where an observer is used to estimate the state of the plant, which can then be used in feedback control. To make an observer robust to inaccuracies of the forward model and to deal with disturbances, there is normally a state correction pathway term based on actual output error calculated as the difference between the actual output and a delayed prediction of plant output. This results in the state prediction based on the efference copy of the motor command being combined with a correction term based on the delayed sensory feedback, something which has been shown to occur during the control of human movement (Wolpert et al., 1995).

Within such an observer-based controller framework, the observer performs state estimation for an active movement using efference copy, while improving the estimate using the delayed feedback signals. In the case of a purely visual observation or passive movement of the arm, the observer can still make a state estimate, but only based on the state corrections from feedback. From the premise that state is the key issue in formation of separate motor memory, such a framework would account for the observation that either active, passive or visual lead-in movements would influence state estimation.

To conclude, we have shown the current and previous observations of lead-in phenomena are consistent with the hypothesis that the human motor system operates as an observer-based controller mechanism, that makes use of a forward model to estimate state. In particular, our results support the proposal (Crevecoeur et al., 2016) that even though the variances of visual positional information is known to be lower than that obtained from proprioception, its longer temporal delay reduces its weighting in state estimation. As a consequence of this, visual information has less effect on the motor system than proprioceptive information, an effect that we have extended to the learning and generalization of opposing dynamics.

Author contributions

ISH and DWF designed and implemented the study. SF performed data collection. ISH performed data analysis. ISH, SF and DWF wrote the manuscript.

Competing interest statement

The authors declare that they have no financial, personal, or professional interests that could be construed to have influenced the paper.

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References

Addou T, Krouchev N, Kalaska JF (2011) Colored context cues can facilitate the ability to learn and to switch between multiple dynamical force fields. Journal of Neurophysiology 106:163–183.

Brashers-Krug T, Shadmehr R, Bizzi E (1996) Consolidation in human motor memory. Nature 382:252–255.

Burdet E, Osu R, Franklin DW, Milner TE, Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. Nature 414:446–449.

Caithness G, Osu R, Bays P, Chase H, Klassen J, Kawato M, Wolpert DM, Flanagan JR (2004) Failure to consolidate the consolidation theory of learning for sensorimotor adaptation tasks. Journal of Neuroscience 24:8662–8671.

Churchland MM, Cunningham JP, Kaufman MT, Foster JD, Nuyujukian P, Ryu SI, Shenoy KV (2012) Neural population dynamics during reaching. Nature:1–8.

Cothros N, Wong J, Gribble PL (2009) Visual cues signaling object grasp reduce interference in motor learning. Journal of Neurophysiology 102:2112–2120.

Crevecoeur F, Munoz DP, Scott SH (2016) Dynamic Multisensory Integration: Somatosensory Speed Trumps Visual Accuracy during Feedback Control. J Neurosci 36:8598–8611.

Donchin O, Francis JT, Shadmehr R (2003) 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.

Franklin DW, Osu R, Burdet E, Kawato M, Milner TE (2003) Adaptation to stable and unstable dynamics achieved by combined impedance control and inverse dynamics model. Journal of Neurophysiology 90:3270–3282.

Gandolfo F, Mussa-Ivaldi FA, Bizzi E (1996) Motor learning by field approximation. Proc Natl Acad Sci USA 93:3843–3846.

Goodbody SJ, Wolpert DM (1998) Temporal and amplitude generalization in motor learning. Journal of Neurophysiology 79:1825–1838.

Hirashima M, Nozaki D (2012) Distinct motor plans form and retrieve distinct motor memories for physically identical movements. Curr Biol 22:432–436.

Howard IS, Ford C, Cangelosi A, Franklin DW (2017) Active lead-in variability affects motor memory formation and slows motor learning. Scientific Reports 7:7806.

Howard IS, Franklin DW (2015) Neural Tuning Functions Underlie Both Generalization and Interference. Gribble PL, ed. PLoS ONE 10:e0131268.

Howard IS, Franklin DW (2016) Adaptive tuning functions arise from visual observation of past movement. Scientific Reports 6:28416.

Howard IS, Ingram JN, Franklin DW, Wolpert DM (2012) Gone in 0.6 seconds: the encoding of motor memories depends on recent sensorimotor States. Journal of Neuroscience 32:12756–12768.

Howard IS, Ingram JN, Wolpert DM (2009) A modular planar robotic manipulandum with end-point torque control. Journal of Neuroscience Methods 181:199–211.

Howard IS, Wolpert DM, Franklin DW (2013) The effect of contextual cues on the encoding of motor memories. Journal of Neurophysiology 109:2632–2644.

Howard IS, Wolpert DM, Franklin DW (2015) The value of the follow-through derives from motor learning depending on future actions. Curr Biol 25:397–401.

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

Hwang EJ, Donchin O, Smith MA, Shadmehr R (2003b) A Gain-Field Encoding of Limb Position and Velocity in the Internal Model of Arm Dynamics. Plos Biol 1:e25.

Hwang EJ, Shadmehr R (2005) Internal models of limb dynamics and the encoding of limb state. J Neural Eng 2:S266–S278.

Karniel A, Mussa-Ivaldi FA (2002) Does the motor control system use multiple models and context switching to cope with a variable environment? Exp Brain Res 143:520–524.

Krakauer JW, Ghilardi MF, Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. Nat Neurosci 2:1026–1031.

Mattar AAG, Ostry DJ (2007) Modifiability of Generalization in Dynamics Learning. Journal of Neurophysiology 98:3321–3329.

Miall RC, Weir DJ, Wolpert DM, Stein JF (1993) Is the cerebellum a smith predictor? J Mot Behav 25:203–216.

Miall RC, Wolpert DM (1996) Forward Models for Physiological Motor Control. Neural Netw 9:1265–1279.

Milner TE, Franklin DW (2005) Impedance control and internal model use during the initial stage of adaptation to novel dynamics in humans. The Journal of Physiology 567:651–664.

Nozaki D, Kurtzer I, Scott SH (2006) Limited transfer of learning between unimanual and bimanual skills within the same limb. Nat Neurosci 9:1364–1366.

Nozaki D, Yokoi A, Kimura T, Hirashima M, Orban de Xivry J-J (2016) Tagging motor memories with transcranial direct current stimulation allows later artificially-controlled retrieval. Elife 5.

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113.

Pandarinath C, Gilja V, Blabe CH, Nuyujukian P, Sarma AA, Sorice BL, Eskandar EN, Hochberg LR, Henderson JM, Shenoy KV (2015) Neural population dynamics in human motor cortex during movements in people with ALS. Elife 4:e07436.

Reinkensmeyer DJ, Burdet E, Casadio M, Krakauer JW, Kwakkel G, Lang CE, Swinnen SP, Ward NS, Schweighofer N (2016) Computational neurorehabilitation: modeling plasticity and learning to predict recovery. J NeuroEngineering Rehabil 13:42.

Sarwary AME, Stegeman DF, Selen LPJ, Medendorp WP (2015) Generalization and transfer of contextual cues in motor learning. Journal of Neurophysiology:jn.00217.2015.

Scheidt RA, Reinkensmeyer DJ, Conditt MA, Rymer WZ, Mussa-Ivaldi FA (2000) Persistence of motor adaptation during constrained, multi-joint, arm movements. Journal of Neurophysiology 84:853–862.

Sheahan HR, Franklin DW, Wolpert DM (2016) Motor Planning, Not Execution, Separates Motor Memories. Neuron 92:773–779.

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

Smith OJM (1959) A controller to overcome dead time. ISA J 6:28–33.

Thoroughman KA, Shadmehr R (2000) Learning of action through adaptive combination of motor primitives. Nature 407:742–747.

Wainscott SK (2004) Internal Models and Contextual Cues: Encoding Serial Order and Direction of Movement. Journal of Neurophysiology 93:786–800.

Wolpert DM, Ghahramani Z, Jordan MI (1995) An internal model for sensorimotor integration. Science 269:1880–1882.

Yeo S-H, Wolpert DM, Franklin DW (2015) Coordinate Representations for Interference Reduction in Motor Learning. Balasubramaniam R, ed. PLoS ONE 10:e0129388.

Yokoi A, Hirashima M, Nozaki D (2011) Gain field encoding of the kinematics of both arms in the internal model enables flexible bimanual action. Journal of Neuroscience 31:17058–17068.