Exp Brain Res (2009) 194:451–463
DOI 10.1007/s00221-009-1720-x

RESEARCH ARTICLE

Multi-compartment model can explain partial transfer of learning within the same limb between unimanual and bimanual reaching

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Received: 12 November 2008 / Accepted: 17 January 2009 / Published online: 11 February 2009

Abstract Multi-limb motor skills, such as swimming and rowing, often involve isolated practice of each limb (unimanual) followed by practice with both limbs together (bimanual). We recently demonstrated that learning a novel load during unimanual reaching is partially, but not completely transferred to the same limb during bimanual reaching (and vice versa), learning can remain hidden and only revealed by the original context, and the ability to learn two conflicting force fields if each was separately associated with unimanual and bimanual reaching (Nozaki et al. 2006). The purpose of the present article is to develop a formal state-space model to conceptualize and interpret these complex experimental results. The model contains three separate compartments for learning, a unimanual-specific, a bimanual-specific, and an overlapping compartment, and the internal state of each compartment is updated context-dependently according to motor errors. The model was able to capture all major aspects of motor learning across these two behaviours and predict further complexities during washout trials when bimanual and unimanual trials are interleaved. We propose that partial, but not complete transfer of motor learning is due to a corresponding partial overlap in neural control processes across these behaviours, and is a general feature of different classes of voluntary motor behaviour, such as postural control, point-to-point reaching, manual tracking and oscillatory movements.

Keywords Motor learning · Reaching movement · Bimanual movement · State-space model · Primary motor cortex · Movement error

Electronic supplementary material The online version of this article (doi:10.1007/s00221-009-1720-x) contains supplementary material, which is available to authorized users.

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Introduction

A common form of sports training is to break down complex whole-body skills into isolated training of its components. For example, swimmers will alternately swim lengths of a pool using one arm while the other arm is maintained straight in front or beside their body (Burke 2002; Finch 2004). Conversely, bimanual motor tasks are used in rehabilitation of stroke subjects to facilitate initial learning in the paretic limb followed by training of unimanual-specific tasks with the paretic limb only (Mudie and Matyas 2000; Cunningham et al. 2002). These training approaches implicitly assume that motor skills learned in one context (unimanual or bimanual practice) will transfer to subsequent performance in another context (bimanual or unimanual performance).

Transfer of learning for the same limb has usually been examined by learning a novel load for a single movement and then quantifying how this learning is transferred to a novel speed, direction or spatial location (Shadmehr and Mussa-Ivaldi 1994; Goodbody and Wolpert 1998; Thoroughman and Shadmehr 2000; Singh and Scott 2003;

Donchin et al. 2003). These studies demonstrate a continuous degradation in the transfer of learning as movement conditions become less similar.

The problem of switching from unimanual to bimanual performance reflects a categorical rather than a continuous change in motor performance: bimanual movements involve temporal coupling across the two limbs (Swinnen 2002). A few studies have examined how learning transfers across contexts such as from point-to-point reaching to drawing movements (Conditt et al. 1997), or transfer from grasping a robot to free arm movements (Cothros et al. 2006). However, the kinematics and/or kinetics of these movements change dramatically across these contexts. The question is whether moving the other arm influences learning associated with the trained arm for the same nominal movement.

We addressed this issue by training subjects to perform unimanual and bimanual reaching movements while a novel force field was applied to only their left (or right) arm (Nozaki et al. 2006). First, we observed partial, but not complete transfer of learning within the same limb between unimanual and bimanual reaching. Second, there was hidden learning that remained intact (but invisible) until the original context was again encountered. Finally, subjects could learn two conflicting force fields simultaneously, when one was paired with unimanual movements and the other with bimanual movements.

The purpose of the present article is to provide a mathematical model to characterize and interpret how these complex patterns of learning and transfer occur across unimanual and bimanual skills. The model divides neural process for motor learning into three compartments, one specific for unimanual, one for bimanual, and a third overlapping compartment for both types of movements. Each compartment has an internal state which is updated (when active in the task) after every movement trial. We illustrate that the model can capture all of the complex features of the learning only when movement error is directly used for updating the state of each compartment.

Models and methods

Compartment state-space model

The present context-dependent model is derived from a basic state-space model previously used to characterize unimanual learning of novel loads during reaching (Fig. 1a; Thoroughman and Shadmehr 2000; Donchin et al. 2003; Smith et al. 2006). This approach assumes that the motor system has its own internal state that is updated according to movement error based on,

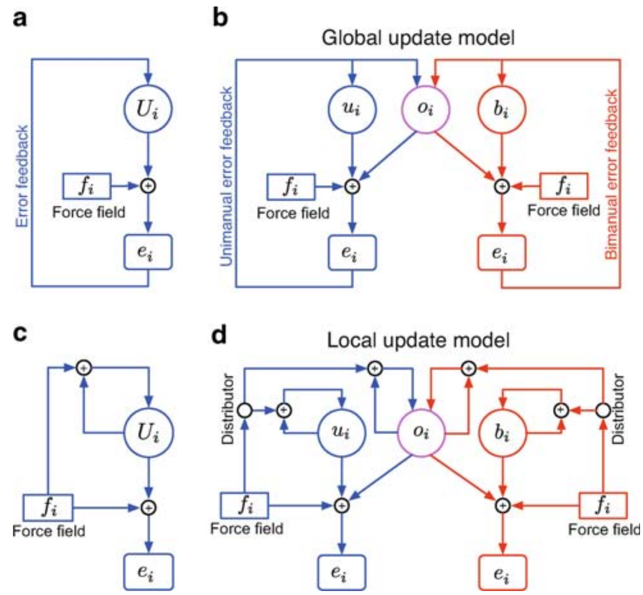

Fig. 1 Configuration of the models. **a** Traditional state-space model where total movement error e, is measured and fed back to update the internal state of the system U. **b** Three compartment model of the motor system where the internal state of the system is denoted by unimanual-only (u), bimanual only (b) and overlapping (o) compartments. In the global update model, both u and o (both b and o) use common information of the unimanual (bimanual) movement error for the updates after unimanual (bimanual) movement trial. **c** Single compartment model where the applied force, f, is combined internally with U and then used to update the system. **d** Extension of model in c to the multi-compartment situation. In this local update model, each compartment active in a task is updated based on its own contribution to the task and the applied force field

$$U_{i+1} = \alpha U_i - K e_i, \tag{1}$$

$$e_i = U_i + f_i, \tag{2}$$

where α and K are constants, and U_i, f_i and e_i denote the internal state, the force field and the movement error for the ith unimanual movement, respectively. Without loss of generality, we assume that these variables are expressed in the same units. The value of α is related to the spontaneous loss (i.e. forgetting) of motor learning, and $\alpha = 1$ means that there is no such loss. K represents a sensitivity of the update of the internal state to the movement error: a large K indicates greater learning or change in the internal state for a given movement error.

We now extend this basic model to consider the situation where two different contexts, unimanual and bimanual movements, utilize partial but not complete control processes. In this situation, the single internal state, U in Fig. 1a, must now be represented by three internal states, u, o and b which denote the internal state for unimanual-specific, overlapping, and bimanual-specific compartments, respectively. The first two states, u and o, participate in unimanual movements, whereas o and b participate in bimanual movements.

An important consequence of generalizing from a single to multiple compartments is how feedback is used to update each compartment. One scenario that leads directly from the structure shown in Fig. 1a is that total movement error is used directly to update each active compartment (Fig. 1b). Hence, we will call this the "global update rule" since errors reflect the total influence of the network output and the applied force field. In this case, the update rule for the the i-th unimanual reaching, updates according to the unimanual error e_i using:

$$u_{i+1} = \alpha u_i - k_1 e_i, \tag{3}$$

$$o_{i+1} = \alpha o_i - k_2 e_i, \tag{4}$$

$$b_{i+1} = \alpha b_i, \tag{5}$$

$$e_i = u_i + o_i + f_i, \tag{6}$$

where k_1 and k_2 are constants. It is important to note in Eqs. 3–6 that only unimanual-specific and overlapping compartments are updated following unimanual movements (analogous equations update o_{i} and b_{i} for bimanual movements). Note that U_i in Eq. 1 is now $u_i + o_i$ in Eqs. 3 and 4, hence K in Eq. 1 needs to be $k_1 + k_2$. Hence, the k_1 and k_2 can be represented as $K(1 - \phi)$ and $K\phi$, respectively, by using a parameter which represents the amount of overlap $\phi(0 \leq \phi \leq 1)$ between unimanual and bimanual processes.

Alternatively, a single compartment model can be reorganized to combine the applied force with the compartment's output internally rather than using total movement error directly (Fig. 1c). In this interpretation, the update of the internal state proceeds until it compensates for the applied force. Performance is identical for the single compartment models shown in Fig. 1a, c. However, this update rule (i.e., force compensation) becomes quite different for multiple compartments. Indeed, Eqs. 3–6 are not the only way decomposing Eqs. 1 and 2 into three compartments. Alternative decomposed model is expressed as:

$$u_{i+1} = \alpha u_i - K\{u_i + (1 - \phi)f_i\}, \tag{7}$$

$$o_{i+1} = \alpha o_i - K(o_i + \phi f_i), \tag{8}$$

$$b_{i+1} = \alpha b_i, \tag{9}$$

$$e_i = u_i + o_i + f_i. \tag{10}$$

For example, this model corresponds to the case when the brain detects the external applied force which should be counteracted (i.e., in this case, the error signal is not the movement error (Eq. 10) but the applied external force) and then distributes it among different compartments according to their size characterized by parameter ϕ. The update for each compartment proceeds independently until the internal state reaches the distributed force level. Each compartment knows its own goal force level only, and thus we will call this model the "local update rule" (Fig. 1d). Analogous equations update o_{i} and b_{i} for bimanual movements.

Subjects and experimental device

Three of the four human experiments have been described in a previous report (Exp. 1–3, Nozaki et al. 2006). Briefly, all experiments were performed with the KINARM robot, a planar robotic exoskeleton that can apply joint- or hand-based loads directly to the limb segments (Scott 1999; BKIN Technologies Ltd, Kingston, Canada). On certain trials we imposed a hand-based velocity-dependent force field to the left arm. This perturbation would result in a large lateral displacement in the absence of any predictive compensation. The robotic device was coupled to a virtual reality system such that start, finger tip, and target positions were projected as small circles on a semi-transparent mirror through which subjects could see their entire limb.

The starting position (1 cm diameter) of the left and right hands were spaced equally from the midline by 6–8 cm, giving shoulder and elbow angles of ~33–42° and 90°, respectively. The target position for each hand was 10 cm forward from the start position. Targets could appear for the left hand alone (unimanual) or for both hands (bimanual) after a 1.5 ± 0.25 s hold time at the start position. Target conditions were pre-cued by one or two vertically long ellipse(s) (0.3 × 8.0 cm) appearing at the starting target(s) for unimanual or bimanual trials, respectively. Subjects were required to reach with a peak hand velocity of 0.4 ± 0.06 m/s. Before data collection, subjects performed 30–40 unloaded practice trials to familiarize themselves with the task.

Behavioural experiments

Experiment 1

This experiment examined the effect of learning a novel load in one behaviour on trials when the load was abruptly removed during both behaviors. Eight subjects completed two counter-balanced sessions where they trained with a velocity-dependent force field (f_x, f_y) during either unimanual reaches or bimanual reaches [$f_x = 10\upsilon_y$ and $f_y = -10\upsilon_y$ (in Newtons) where the υ_y is forward velocity (m/s) of the finger tip].

Each session began with 20 unloaded unimanual and bimanual movements for a pre-perturbation baseline. For the unimanual condition, subjects then performed 40 reaches with the force field applied to the left arm during unimanual reaching. Training was followed by 120 trials where the force field was randomly removed once per 12 trials, i.e. 'catch trials'. Catch trials either involved unimanual or bimanual reaching allowing us to compare transfer from unimanual training to bimanual reaches. The session ended with 20 repeated unloaded unimanual reaching movements to observe washout of the learning. The bimanual condition followed a similar pattern of trials.

Experiment 2

This experiment examined how washout trials in one behaviour could not remove all learning generated in the other behaviour. Eight subjects completed two counter-balanced sessions similar to the 20 baseline trials, 40 training trials, and 120 test/random-catch trials of Experiment 1. As before, perturbations were applied only to their left arm. Subjects then had two blocks of washout trials −10 repeated bimanual (or unimanual) washout trials followed by 10 repeated unimanual (or bimanual) washout trials for the unimanual (or bimanual) training.

Experiment 3

This experiment examined adaptation to conflicting force fields each presented selectively with unimanual and bimanual reaching trials. Ten subjects completed two sessions in counter-balanced order: ‘combined’ and ‘unimanual-only’. In the ‘combined’ session, subjects reached with unimanual and bimanual movements in alternation. Subjects began with 20 baseline trials of both movement types (40 trials total) followed by 80 training trials where rightward ($f_x = 10\upsilon_y$ and $f_y = -10\upsilon_x$; υ_x and υ_y are rightward and forward velocity of the finger tip, respectively) and leftward ($f_x = -10\upsilon_y$ and $f_y = -10\upsilon_x$) force fields were also alternated on each trial. As a result, the force field applied to the left limb during unimanual reaches was opposite the force field during the bimanual reaches. In the following 120 trials, unimanual and bimanual catch trials were interleaved once per 12 trials (i.e. 10 sets). Bimanual and unimanual catch trials were performed in the 6th and 11th of each set. The session ended with 40 catch trials that again alternated between movement types. Subjects were not given any explicit information on the direction of the force fields.

In the ‘unimanual-only’ condition, subjects performed only unimanual reaches. Following 20 baseline trials, subjects were exposed to the opposing fields in alternating trials, 80 in total. Force field direction was precued by the target color (blue rightwards, red leftwards). As in the combined condition, catch trials for each target color were interleaved in the following 120 trials. The session ended with 20 repeated catch trials for each target color.

Experiment 4

This experiment specifically examined performance when alternate unimanual and bimanual washout trials were performed following learning in one of these contexts. Fifteen subjects completed two counter-balanced sessions. Subjects began each experiment with 20 baseline trials in both contexts, and then performed 80 training trials in one context (unimanual or bimanual). The rightward force field (the same as in Experiment 3) was applied to the left arm. Movement distance was set to 15 cm. Following the training trials, washout trials were performed sequentially for each context (i.e. unimanual then bimanual) starting with the non-training context (20 trials for each).

Data analysis

The angular position and velocity data of the motor resolvers were collected at 1,000 Hz. Signals were resampled at 100 Hz then filtered with a fourth order zero-phase-shift Butterworth filter (effective cut-off frequency of 8 Hz). Finger position and velocity was calculated from this angular data. We quantified movement accuracy as the lateral deviation of the hand at its peak velocity relative to a line connecting the start and target positions.

Estimation of model parameters

The parameters for each model were calculated from the results of Experiment 1. Since we used a constant force field f for the learning phase, we can compute U_i as:

$$U_i = (\alpha - K)^{i-1}\left(U_1 + \frac{K}{1-\alpha+K}f\right) - \frac{K}{1-\alpha+K}f, \tag{11}$$

where U_1 is the initial condition and it is assumed to be zero. Hence, the unimanual movement error of the ith trial is

$$e_i = U_i + f = \frac{K(\alpha-K)^{i-1}}{1-\alpha+K}f + \frac{1-\alpha}{1-\alpha+K}f. \tag{12}$$

For the first loaded trial, e_1 is f, hence, the movement error normalized by the error of the first trial is

$$\frac{e_i}{e_1} = \frac{K(\alpha-K)^{i-1}}{1-\alpha+K} + \frac{1-\alpha}{1-\alpha+K}. \tag{13}$$

First, the values of α and K were identified by fitting Eq. 13 to the data of the learning phase of experiment 1 (first 40 trials with loads for each of the 8 subjects) using the Levenberg-Marquardt algorithm (Press et al. 2007). The calculation of ϕ was based on the ratio of the magnitude of the aftereffect for the catch trials between unimanual and bimanual movements. It should be noted that the ratio does not directly reflect ϕ. Specifically, Experiment 1 was simulated using Eqs. 3–6 or Eqs. 7–10 for various values of ϕ ranging from 0 to 1 with increments of 0.05. The initial value of each state was set to 0 and the force field f_i was set to 0 for the baseline, catch trial, and washout and 1 for the learning phase (The setting was the same as in the simulation of Experiments 2–4. In the simulation of Experiment 3, the leftward force field was set to −1). For each ϕ, the simulation was repeated 100 times (The large number of repeat trials was required to average out the effects of the random order of the catch trials). Then, a relationship between ϕ and the ratio of bimanual aftereffect to unimanual aftereffect was constructed. The ϕ that best matched the experimentally observed ratio across these two contexts in Experiment 1 was selected. An analogous process was performed for bimanual learning. These identified parameters were maintained fixed in for comparisons with Experiments 2–4.

Results

Experiment 1: variation in unimanual and bimanual catch trials and model fitting

As shown previously (Nozaki et al. 2006), the applied force led to significant rightward errors on the initial reach followed by a return to the baseline movement pattern within 40 trials (Fig. 2a). When subjects trained on unimanual movements they showed smaller bimanual aftereffects than unimanual aftereffects. As well, there was an increase in deviation of the hand in non-catch trials when catch trials were introduced after trial 40. Finally, unlearning of the force field when the load was removed (washout) required less than 10 trials. Identical results were observed when subjects trained on bimanual movements (Nozaki et al. 2006).

The parameters for the context-dependent compartment model were estimated by curve fitting as $\alpha = 0.94 \pm 0.03$ and $K = 0.37 \pm 0.18$ for unimanual learning and as $\alpha = 0.99 \pm 0.01$ and $K = 0.19 \pm 0.06$ for bimanual learning (These values represent the estimated coefficients and their 95% confidence interval). There was no significant difference in the confidence of these parameters across unimanual and bimanual conditions ($P > 0.05$ by t test), so we decided to adopt the values obtained from the averaged learning curve ($\alpha = 0.97$ and $K = 0.28$; see supplementary Fig. 1a). For the global update rule, the estimated ϕ was 0.83 and 0.72 for unimanual and bimanual movement, respectively. In contrast, for the local model, the estimated

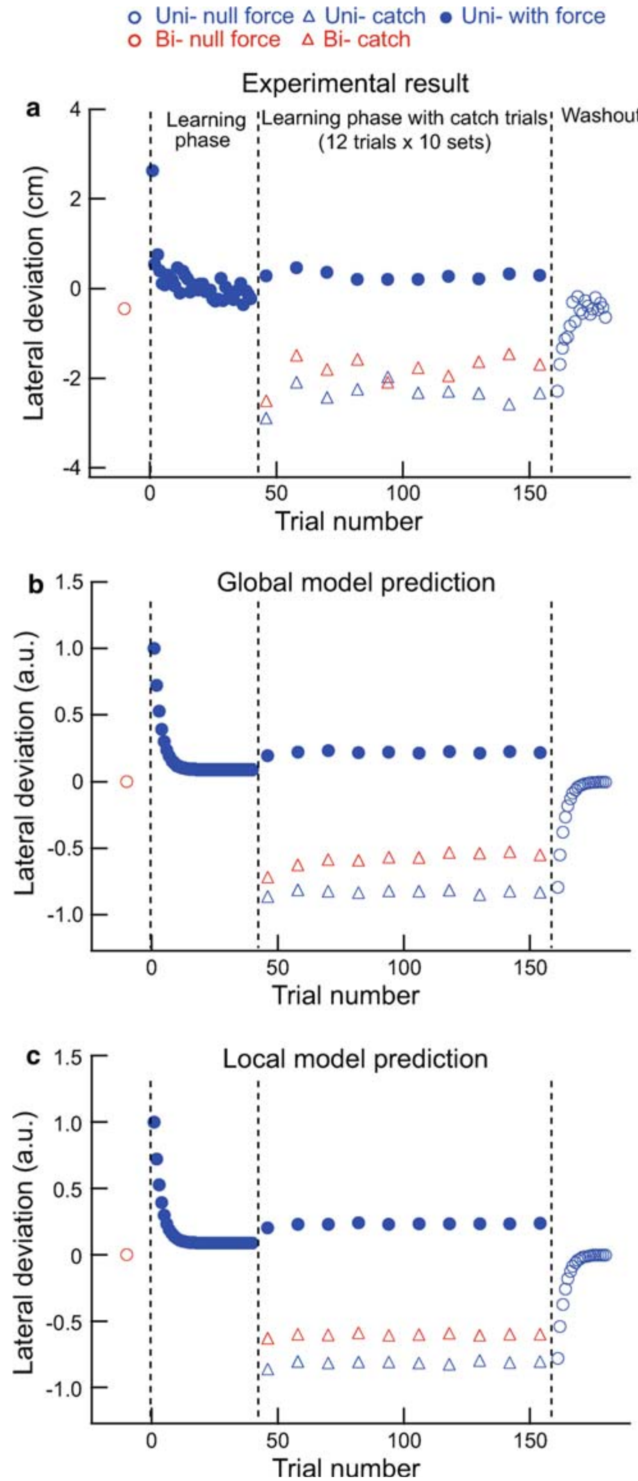

Fig. 2 Trial-by-trial changes in lateral hand deviation in Experiment 1. **a** Experimental result. The values are the mean for each trial (learning and washout phase) and for each block consisting of 12 trials (learning phase with catch trials) across 8 subjects obtained in our previous study (Nozaki et al. 2006). **b**, **c** Mathematical prediction by the 3 compartments model with global (**b**) and local (**c**) update rule. See results for the parameters used

ϕ was 0.71 and 0.57 for unimanual and bimanual movement, respectively (Supplementary Fig. 1b).

Figure 2b, c illustrate the simulated results for the unimanual learning condition. Virtually identical results were observed whether using the global or local update rule. That is, each simulation predicted (1) the time-dependent behavior during learning and washout (2) the degree of transfer for unimanual and bimanual catch trials and (3) the slight degradation in performance during loaded reaching when catch trials were introduced after 40 trials.

Although the global and local update rules provide similar behavioural predictions (Fig. 3a, b), there are substantive differences in the underlying pattern of activity for each of the compartments (Fig. 3c, d). For both update rules, learning is initially isolated to the unimanual-specific and the overlap compartments for the initial 40 learning trials. However, this changes when bimanual catch trials are subsequently introduced. In a catch trial, there is no applied force and the hand deviates in the opposite direction due to the contribution of the overlapping compartment. This movement error leads to an update of the bimanual-specific compartment in the global update rule (Fig. 3c), but no changes when the local update rule is implemented (Fig. 3d).

Experiment 2: hidden learning

The repeated presentation of catch trials normally leads to a washout of force field learning within $\sim$10 trials (see Fig. 2a). Figure 4a displays the results of Experiment 2 illustrating that two separate phases of washout can occur if subjects are trained with loads for unimanual movements, and then washout trials are performed first for bimanual movements and then for unimanual movements. The first ten washout trials without loads show the classic pattern of reduced hand deviations in each subsequent trial. Following these ten trials, the first unimanual movement (also without a load) displayed an increase in hand deviation from the last bimanual washout trial. It appears that some of the unimanual learning remained intact and was 'invisible' until the proper probe, unimanual reaching, was again performed. Identical results were obtained for bimanual learning with initial unimanual washout: subjects re-expressed aftereffects with bimanual washout trials (Nozaki et al. 2006).

Our context-dependent compartment model captures this double washout pattern (Fig. 4a). Both the global and local update rules predict this pattern of behaviour although the global model predicts larger aftereffects for the unimanual washout (Fig. 4a). This was due to different patterns of activity in the three compartments (Fig. 4b, c). For the local update rule, washout of learning during the bimanual trials is provided exclusively by the overlap compartment. The unimanual-specific compartment retains most of its activity throughout this initial block of washout trials, with only a small decay in its magnitude due to parameter α (Fig. 4c). In contrast, the global update rule shows a more complex interaction between the activity in the bimanual-specific and the overlap compartments (Fig. 4b). The former shows a shift from baseline levels at the start of the washout trials which grows in magnitude

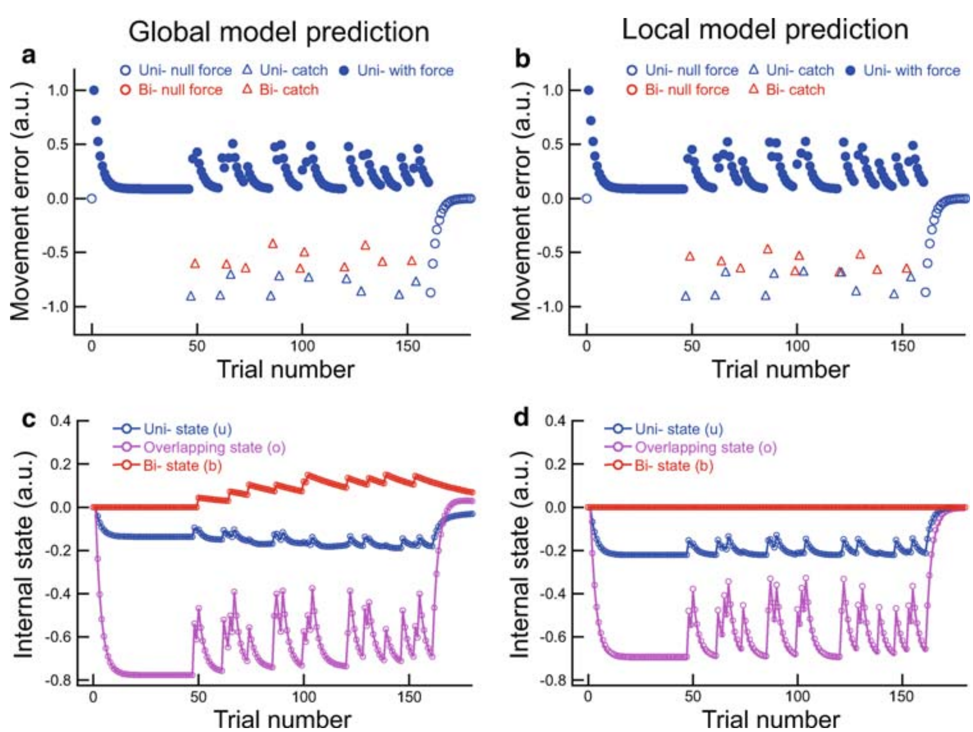

Fig. 3 Sample trial-dependent behavior of movement error simulated by the three compartments model with global (**a**) and local (**b**) update rules. Unimanual and bimanual catch trials were performed on the same trials for both cases. **c**, **d** Corresponding behavior of the internal state for each compartment

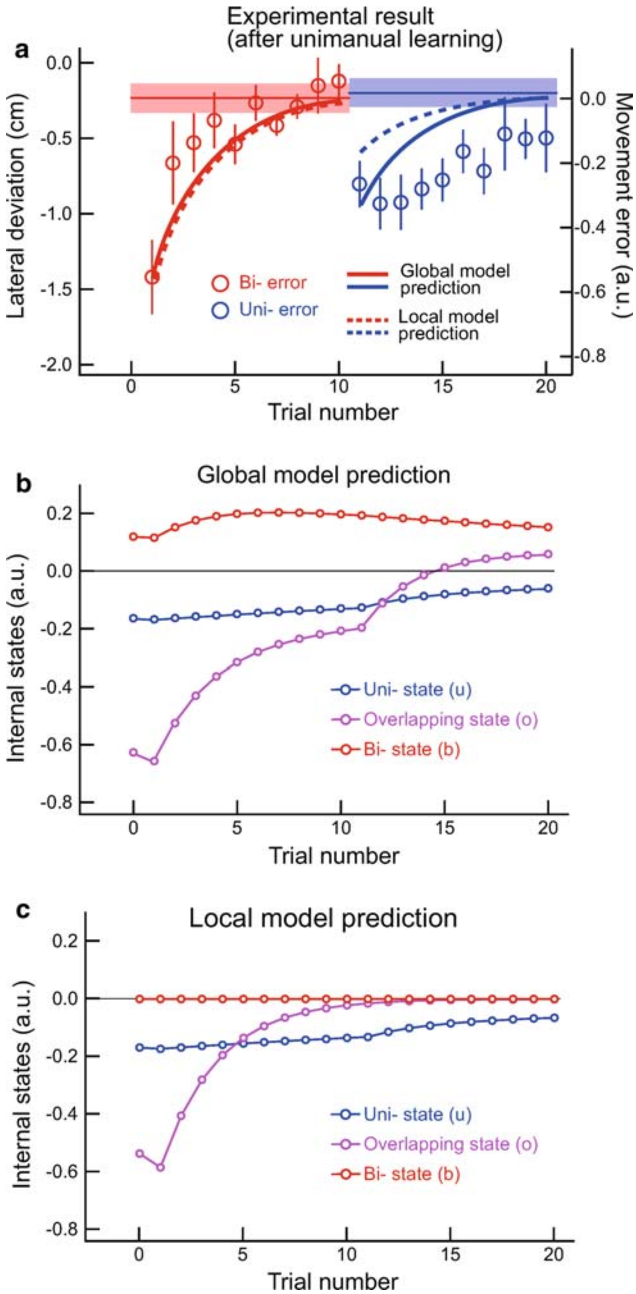

Fig. 4 Sequential blocks of bimanual and unimanual washout trials after unimanual learning. **a** Experimental result observed in Nozaki et al. (2006) along with corresponding predicted behaviour from each model. **b**, **c** Pattern of activity in each compartment for global (**b**) and local (**c**) update rules. The parameter values were the same as the ones used in Fig. 2

over the next few trials. The zero movement error at the end of bimanual washout trials was not due to the loss of memory but due to the balance of the memories between bimanual-specific and overlapping compartments (See also Smith et al. 2006). Therefore, the overlapping compartment still retained substantial amount of motor learning (Fig. 4b), which caused the larger aftereffect for the subsequent unimanual washout (Fig. 4a).

Experiment 3: learning conflicting force fields

Adaptation to two conflicting force fields presented in alternation is normally extremely difficult to learn (Gandolfo et al. 1996; Osu et al. 2004; Shadmehr et al. 2005). In fact, during this 'combined' condition, subject's exhibited partial adaptation to the conflicting force fields (Fig. 5a). The difference in lateral hand deviation between rightward and leftward force fields (compensation) gradually decreased during the learning phase. In addition, significant aftereffects were observed during the washout phase. In contrast, when subjects reached unimanually while the conflicting force fields were explicitly cued ('unimanual-only' condition; Fig. 5b), they exhibited no significant compensation, and significantly smaller aftereffects.

These differences in learning for 'combined' and 'unimanual-only' conditions are captured with our multi-compartment model using the global update rule (Fig. 5c, d). This version of the model captured (1) the partial learning of the load during the initial learning phase (2) opposing hand deviations during catch trials for the 'combined' learning and (3) opposing hand deviations for the washout phase of the task (Fig. 5c). As well, it predicted minimal evidence of learning for the 'unimanual-only' condition (Fig. 5d). In contrast, the version of the three compartment model using a local update rule failed to capture any substantial learning of the loads, and only very modest aftereffects during catch trials for the combined learning condition (Fig. 5e). The behavior of the unimanual-only condition for the local update rule was the same as the one for the global update rule (Fig. 5f).

These differences in performance for the two versions of the model can be better understood by observing the substantive differences in the activity of the three compartments. For both rules, the alternation of two opposing force fields causes very little learning to occur in the overlapping compartment (Fig. 6). However, the global update rule (Fig. 6a) permits far greater learning to be created in the context-specific compartments than permitted by the local update rule (Fig. 6b). The local update rule could match the observed pattern of learning in this experiment, but only by reducing the size of overlapping compartment ϕ to approximately half its size, 0.35 from 0.71 to 0.57 (See supplementary Fig. 2). The strength of the model with the global update rule is that all of its parameters were set in Experiment 1.

We were particularly intrigued by how washout trials varied across Experiment 1 and 3. Figure 7a expands the results for the washout trials for unimanual learning and washout from Experiment 1 and the washout trials for the 'combined' learning task in Experiment 3. In the former case, washout normally is complete within $\sim$7 trials [no

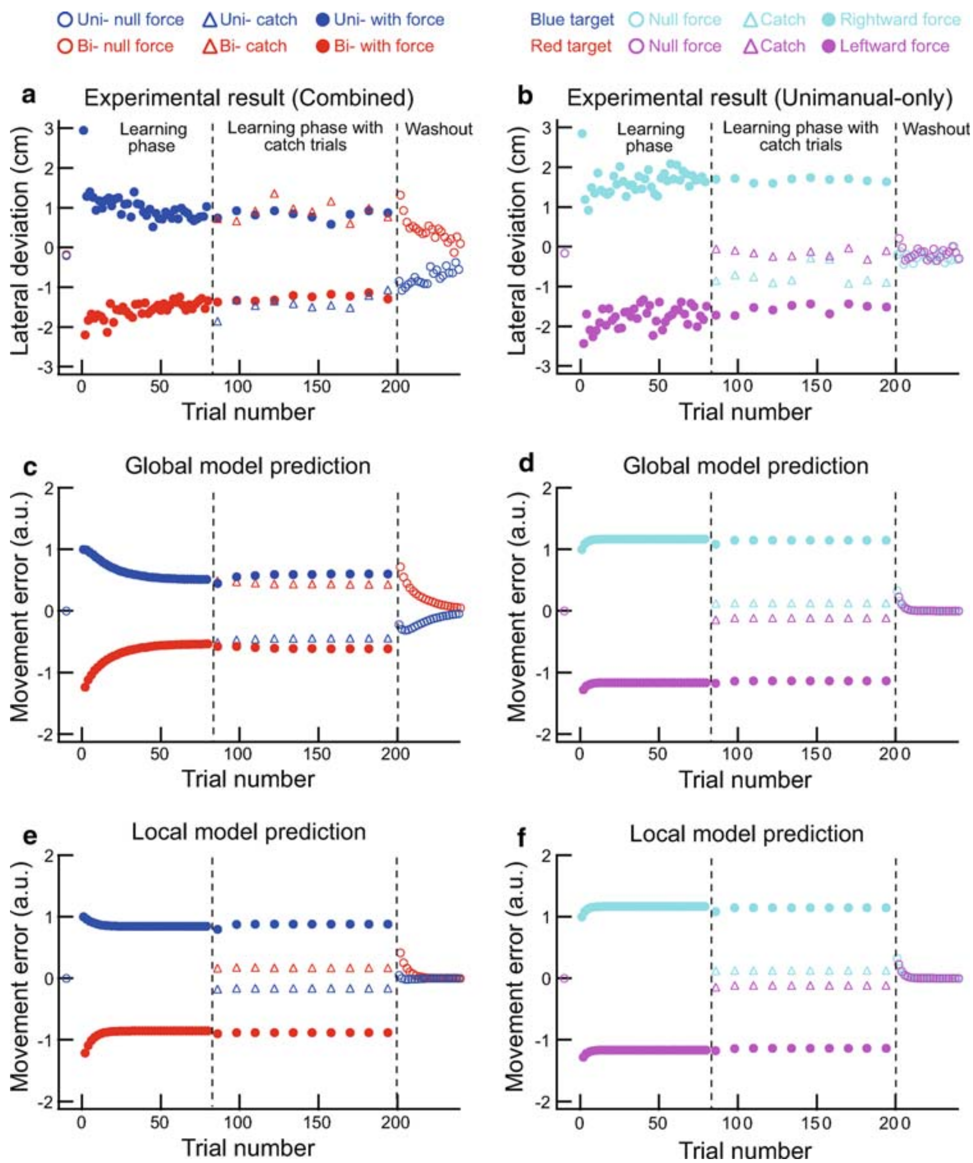

Fig. 5 Trial-by-trial changes in movement error for combined and unimanual-only conditions. **a**, **b** Experimental result observed in Experiment 3 for combined (**a**) and unimanual-only condition (**b**). The positive and negative values indicate, respectively, rightward and leftward movement error. **c**, **d** Model prediction for combined (**c**) and unimanual-only condition (**d**) when the global update rule was adopted. **e**, **f** Model prediction for combined (**e**) and unimanual-only condition (**f**) when the local update rule was adopted. Parameters for 'combined' learning set in Experiment 1, whereas ϕ was changed to 1 (i.e. full overlap) in the simulation of unimanual-only condition

significant difference from baseline after the 7th washout ($P > 0.05$ by z test)]. However, there are still substantial aftereffects after 20 washout trials (for each context) during the 'combined' condition [significantly different from baseline ($P < 0.05$ by z test) except for the 18th bimanual and for the 19th unimanual washout trial].

A similar difference in washout trials was predicted for the multi-compartment model with the global update rule. Washout of learning required $\sim$10 trials following unimanual learning (Fig. 2b), but required many more trials following 'combined' learning (Fig. 7b). The extended time required for washout trials during the 'combined' learning task was generated by an interaction between the overlapping and context-specific compartments (Fig. 7c). This interaction moved the state of the overlap compartment back-and-forth around zero, which slowed the washout of learning in the context-specific compartments. The local update rule failed to show an extended washout period following 'combined' learning and displayed aftereffects in only one of the two contexts (Fig. 7d, e). This is because washout of learning of each compartment is independent of the others so each retains the same basic decay in learning. Such elongation of washout was never reproduced for any value of ϕ using the local update rule (see supplementary Fig. 2).

The multi-compartment model permits us to examine how the size of the overlap compartment can influence learning during 'combined' learning. Figure 8a illustrates this pattern of learning when ϕ is set at three different values. Full overlap ($\phi = 1.0$) means that there is no task specific compartment and only one common overlapping compartment that is responsible for learning during both

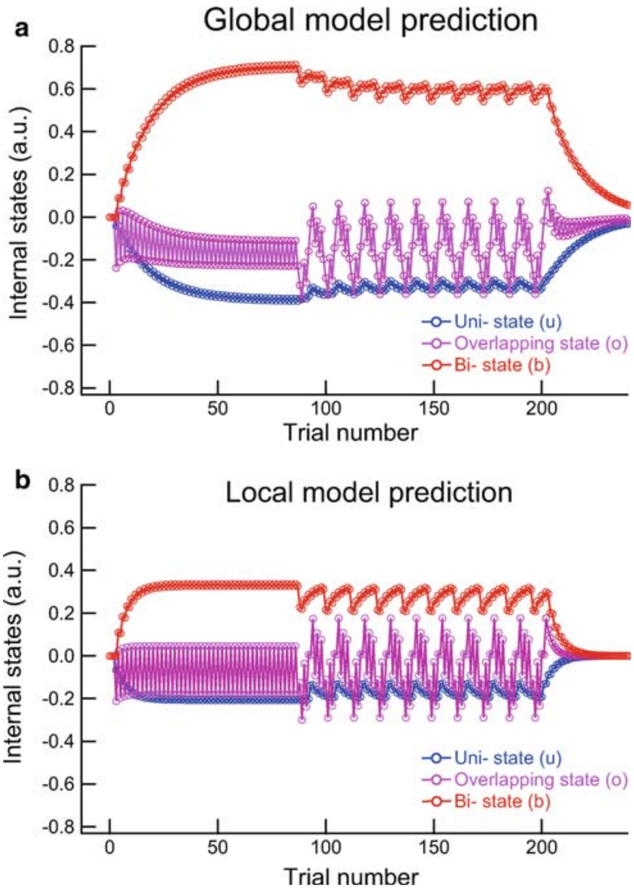

Fig. 6 Predicted trial-by-trial changes in the internal state for each compartment during combined learning. Model results with global (**a**) and local (**b**) update rules for Experiment 3 when training began with a bimanual trial

unimanual and bimanual tasks. Essentially no learning occurs for this situation. In contrast, no overlap ($\phi = 0$) means that the system possesses only two specialized compartments and no overlapping compartment. Substantial learning occurs in each context and learning is again washed out after 10 trails (Fig. 8b). The pattern of learning becomes more complex for any value of ϕ between these extremes. Substantial overlap ($\phi = 0.8$) permits a lot of learning, but washout of learning for interleaved trials is remains relatively high after 10 washout trials. Figure 8b highlights that final movement error and the amount of washout remaining after 10 trials both increase with ϕ, but this coupling reverses when ϕ approaches 0.8. Thus, there is nonlinear relationship between the rate of learning and unlearning when unimanual and bimanual trials are interleaved.

Experiment 4: predicted complexity during interleaved washout trials following single context learning

Based on our model, we predict a further complexity will be present for human subjects in washout trials in which learning is first performed in one context (unimanual or bimanual; 80 trials) and then washout trials are performed sequentially for each context (20 trials for each). Hand deviation during washout trials in a single context normally follows a characteristic decay process attaining baseline measures within ~10 trials (e.g., see Fig. 2). In contrast, the model predicts that after learning in one context, sequential switching between unimanual and bimanual movements during washout trials will create an oscillation or zigzag pattern across the two types of movements: the untrained movement showing less hand deviation than the following trained movement (Fig. 9a). A second subtle effect is that washout trials for the untrained movement should actually overshoot the baseline pattern of hand motion around the fifth washout trial.

Figure 9b indicates the behaviour of washout trials for these interleaved washout trials averaged across all subjects and both sessions (i.e., 30 data sets). There are two notable points. First, the washout process seems to progress quite differently between one context and another context. The aftereffect of the washout trial performed in the non-trained context was significantly smaller ($P < 0.05$ by paired t test) than that of the following washout trial performed in the trained context except for the 1st and 2nd washout trials, leading to a zigzag pattern in accordance with the model prediction. Secondly, significant ($P < 0.05$ by z test) overshoot of the aftereffect was observed in some trials for the non-trained context (10th and 16th trials).

Discussion

We present here a mathematical model to conceptualize the transfer of learning within the same limb across two behavioural contexts, unimanual and bimanual reaching. It has been proposed that the motor system may use multiple compartments or internal models to control motor actions (Wolpert and Kawato 1998; Lackner and DiZio 2005), although the emphasis has been to understand how the motor system manages different mechanical loads/conditions within the same motor behaviour. The present model highlights how different motor behaviours, unimanual versus bimanual movements, appear to be parcellated across multiple compartments in the motor system.

The use of a global update rule captured virtually all aspects of learning and unlearning across the behaviours. Importantly, the model parameters were based on Experiment 1, but the model could predict the results for the other three experiments. The ability to observe the state of each compartment illustrates how interactions within a network can lead to intricate patterns of learning. In particular, the overlapping compartment creates interactions across the two contexts influencing both the learning and unlearning

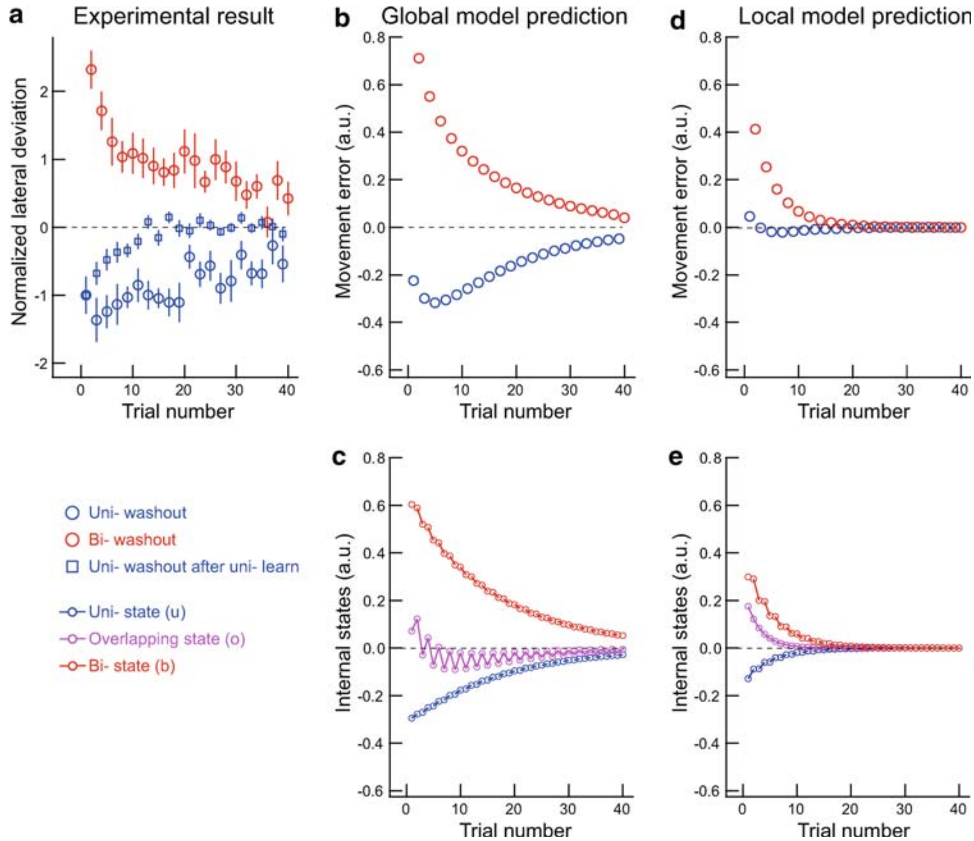

Fig. 7 Slow washout behaviour observed in combined learning condition. **a** Experimental result of lateral hand deviation at peak velocity for unimanual and bimanual washout trials performed alternately after combined learning. As a reference, unimanual washout behavior after unimanual learning is superimposed. The values were normalized using the 1st unimanual movements. **b**, **c** Model prediction for movement errors using the global update rule (**b**) and the internal state for each compartment (**c**). **d**, **e** Model prediction for movement errors using the local update rule. (**d**) and the internal state for each compartment (**e**)

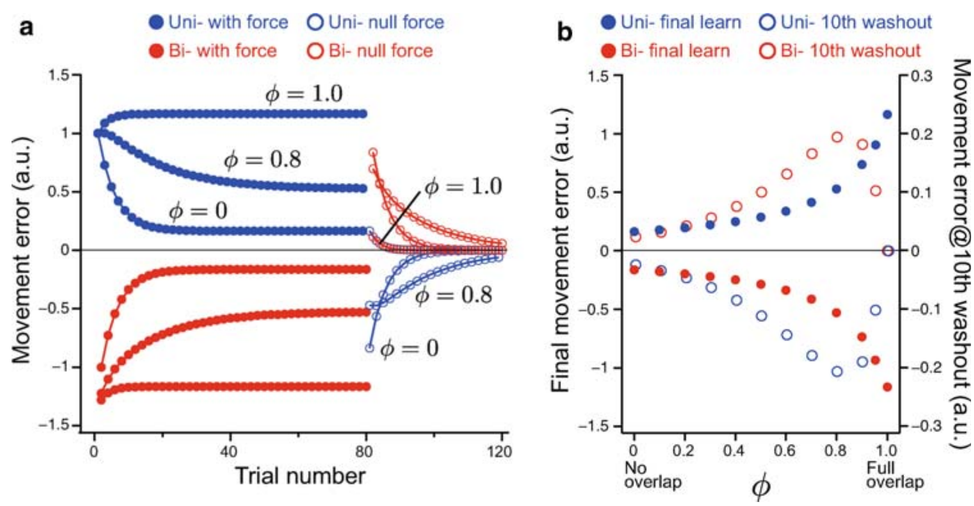

Fig. 8 Influence of the degree of overlap on motor learning behavior. **a** Predicted behavior of motor learning for combined learning condition. The simulation was performed using Eqs. 3–6 with three different values used for the parameter ϕ. The other parameters are the same as in Fig. 2. Initial 80 trials and the following 40 trials are learning and washout phase, respectively. **b** Relationship between the degree of overlap and the final movement error (*left axis*) and the movement error at the 10th washout trial (*right axis*)

phases of the task. This interaction creates unintuitive behavior such as the slow washout after combined learning in Experiment 3 (Figs. 7, 8) and a zig-zag pattern of washout with overshoot in Experiment 4 (Fig. 9). The complexities demonstrated in the model help to explain why the schedule and/or variety of training can influence motor learning (Schmidt and Lee 2005).

The extension from a single to a three compartment model created two potential update rules for considering motor errors. The local update rule assumes updates of the state are performed independently for the three compartments. Such a process explains most of the observed patterns (Figs. 2, 4), except for the behaviour in Experiment 3 (Figs. 6, 7). In contrast, the global update rule assumes a common movement error signal is used to update all task-relevant compartments. This rule captures all the observed patterns of learning and unlearning including slow washout following ‘combined’ learning. The washout performed in alternation of two contexts was unlikely to cause slow washout because it was not observed

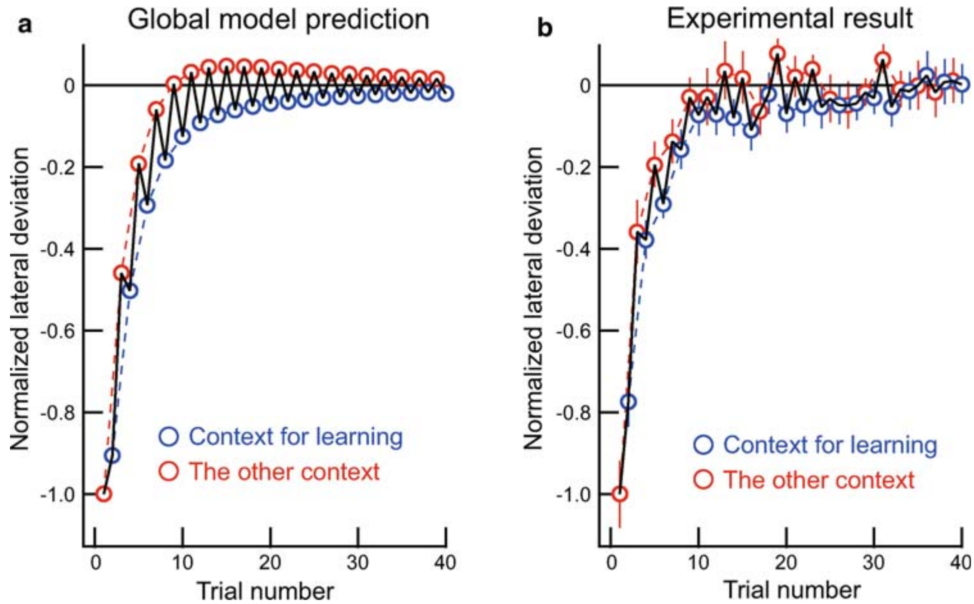

Fig. 9 Trial-by-trial behavior of washout performed with two alternating contexts (i.e. unimanual and bimanual movements) after learning in one context. **a** Global model prediction with the parameters set in Experiment 1. The data were averaged between the two cases (1) alternate unimanual bimanual washout trials after bimanual learning and (2) alternate bimanual unimanual washout trials after unimanual learning. **b** Experimentally observed trial-by-trial changes in lateral hand deviation. The data were mean ± sem calculated across 30 sessions (15 subjects × 2 sessions)

in Experiment 4 (Fig. 9b). Hence, slow washout after 'combined' learning provides strong behavioural evidence that the motor system uses a common signal of movement error to update all active compartments.

Bimanual movements require substantive interhemispheric interactions (Geffen et al. 1994; Swinnen 2002; Aramaki et al. 2006) and intrahemispheric control (Tanji et al. 1988; Donchin et al. 1998, 2002) to coordinate the two limbs. The temporal patterns (onset and termination) of bimanual movements are coupled even if the magnitude of movement varies across the limbs (Kelso et al. 1979a, b). Therefore, bimanual movements possess additional control processes beyond unimanual movements.

We found that learning was restricted to changes in the control of a single limb for both unimanual and bimanual movements. First, learning in our study was restricted to the (left) arm exposed to the applied load with no observed changes in the motion of the other (right) arm for bimanual learning or bimanual catch trials (See Nozaki et al. 2006). Similarly, simultaneous learning of novel loads with both limbs does not cause interference between the limbs (Tcheang et al. 2007). Of course, certain aspects of motor learning acquired by one limb can be transferred to another limb (DiZio and Lackner 1995; Wang and Sainburg 2003, 2004; Criscimagna-Hemminger et al. 2003). Our point is that accidental (and inappropriate) transfer between the limbs did not occur. Second, partial transfer of learning occurred in both directions, from unimanual to bimanual movements, and vice versa. Specifically, our three compartment model suggests that some neural processing is specialized for unimanual movements and does not participate during bimanual movements. Thus, the additional neural processing required for coordinating bimanual movements may explain why only some learning transfers from bimanual to unimanual movements, but it does not explain the reverse.

The three compartment model explicitly posits that there is a shift in the control of a single limb across behavioural contexts, in this case, unimanual versus bimanual movements. Substantive changes in the activity of neurons in MI have been observed across unimanual and bimanual movements although this was interpreted as evidence that MI participated in the control of both contralateral and ipsilateral behaviours and/or bimanual coordination (Donchin et al. 1998, 2002). We propose that MI is predominantly involved in contralateral control, but there is a shift in the population of neurons involved in controlling the contralateral limb. This is consistent with the anatomical evidence that the corticospinal tract projects ~90% contralaterally, and thus is predominantly involved in only contralateral motor control (Porter and Lemon 1995; Lacroix et al. 2004).

A more specific demonstration that neural processing in MI changes across motor behaviours was shown when comparing the load-sensitivity of neurons during posture and movement (Kurtzer et al. 2005). Some neurons responded to loads applied to the limb only during posture, or only during movement, whereas other neurons respond to loads during both posture and movement, to varying degrees. In other words, the shift from posture to movement creates a change in how neurons in motor cortex process information; some neurons are selective for one behaviour, whereas other neurons participate in multiple behaviours. This has important implications for learning because it has been shown that load-related activity changes in MI when non-human primates learn novel loads (Li et al. 2001).

Taken together, we posit that context-dependent shifts in load representations in MI also occur between unimanual and bimanual control. As a result, transfer of motor learning between unimanual and bimanual contexts is provided by a sub-population of neurons that are load-sensitive in both contexts, leading to a limited transfer of learning (Experiment 1). In contrast, neurons that are predominantly load-sensitive in only one context permit learning to be retained in one context after unlearning has occurred in the other (Experiment 2) and simultaneous (though partial) learning of two conflicting force fields (Experiment 3). Based on our observed changes in load-sensitivity of MI neurons across posture and movement, we predict that learning will be only partially transferred across these behaviours. In contrast, we predict that learning can be transferred to another behavioural context if the load representation is retained in this same population of neurons, such as across single- and multi-joint loads during reaching (Gribble and Scott 2002).

We demonstrate a categorical change in behaviour, unimanual versus bimanual movements, leads to a partial, but not complete transfer of learning. Our observations are likely related to previous work illustrating that the transfer of learning during movement varies based on changes in direction or speed (Goodbody and Wolpert 1998; Thoroughman and Shadmehr 2000; Donchin et al. 2003). Speed and movement direction vary along a continuum and the transfer of learning decreases for greater differences between the training and test movements. These observations on the gradual decline in the transfer of learning can be explained based on the response properties of neurons in MI. Thoroughman and Shadmehr (2000) illustrated that the transfer of learning across movement direction followed a cosine function, reminiscent of the broad tuning of MI neurons during reaching (Georgopoulos et al. 1982). Interestingly, a recent study illustrated that a change in movement speed shifts the tuning properties of cells in MI (Churchland and Shenoy 2007) and may explain why the transfer of learning is influenced by movement speed (Kitazawa et al. 1997; Goodbody and Wolpert 1998).

The above description is based only on neural processing in MI, but the link between motor learning and MI activity also reflects neural processes elsewhere in the voluntary motor circuit. Motor learning involves many brain regions including cerebellum (Kawato and Gomi 1992; Imamizu et al. 2000; Maschke et al. 2004) and many cerebral cortical regions (Wise et al. 1998; Sanes and Donoghue 2000; Li et al. 2001; Muellbacher et al. 2002; Padoa-Schioppa et al. 2002; Diedrichsen et al. 2005). There are large changes in activity across multiple cortical regions observed between discrete and oscillatory (rhythmic) wrist movements (Schaal et al. 2004). We predict that such changes in neural processing will lead to partial, but not complete transfer of learning across these contexts.

Practically, the present results have implications regarding the efficacy and limits on the transfer between unimanual and bimanual skills in sports and rehabilitation. Isolated practice of a single limb permits athletes or patients to focus their attention on specific details of motor performance. Here we show that such skill development can be transferred partially to more complex tasks, but that full transfer may never be possible due to constraints on how the brain controls unimanual and bimanual movements. Thus, maximal performance of complex multi-limb skills necessarily requires practice of the task in its entirety. Correspondingly, rehabilitation may be facilitated by bimanual motor practice (Mudie and Matyas 2000; Cunningham et al. 2002) but requires further unimanual training to maximize motor recovery.

Acknowledgments We thank members of the Scott lab for helpful comments, and K. Moore for expert technical help. This work was supported by KAKENHI (#18500456, #20670008) and a CASIO Science Promotion Foundation to D.N., and a grant from the National Science and Engineering Research Council to S.H.S. S.H.S is co-founder and CSO of BKIN Technologies, which commercializes the robotic technology used in this study.

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