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Limited transfer of learning between unimanual and bimanual skills within the same limb

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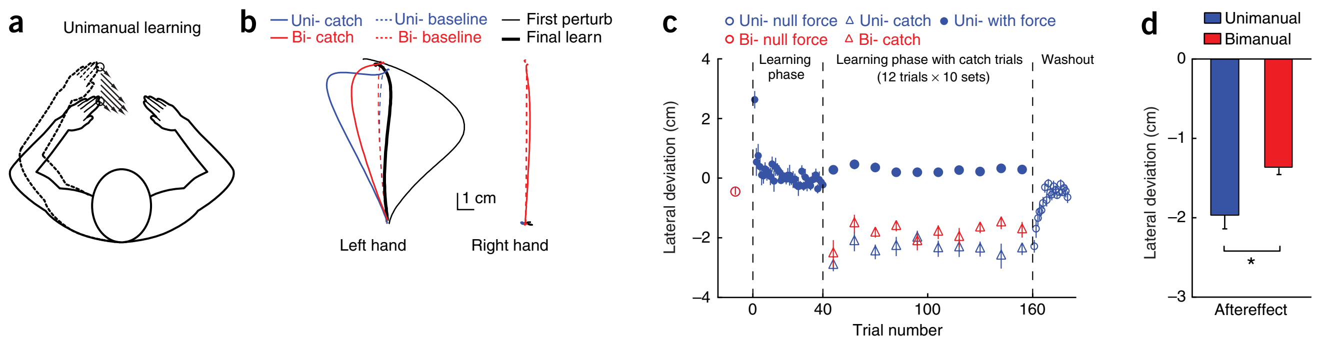
Although a limb's motion appears to be similar across unimanual and bimanual movements, here we demonstrate partial, but not complete, transfer of learning across these behavioral contexts, hidden learning that remains intact (but invisible) until the original context is again encountered, and the ability to associate two conflicting force fields simultaneously, one with each context. These results suggest partial, but not complete, overlap in the learning processes involved in the acquisition of unimanual and bimanual skills.

A common form of sports training is to break down a complex whole-body skill into isolated training of the skill's components. For example, swimmers will alternately swim lengths of a pool using one arm while the other arm is maintained straight in front[1]. This training approach assumes that motor skills learned from one context (unimanual practice) will transfer to subsequent performance in another context (bimanual performance). Here we address the efficacy of learning across these behavioral contexts.

We trained right-handed human subjects to reach with their left arm against an unfamiliar force field delivered by a bilateral robot (**Fig. 1** and ref. 2, KINARM, BKIN Technologies; details in **Supplementary Methods** and **Supplementary Fig. 1** online). All experiments were approved by the Queen's University Human Ethics Committee. Consistent with previous studies[3,4], the applied force led to substantial rightward deviations on the initial reach, followed by a return to near-baseline movement patterns within 40 trials (**Fig. 1b**,**c**). We then tested motor adaptation by removing the force field (that is, in 'catch trials') and observing any leftward deviations of the arm (that is, 'aftereffects'). The aftereffect's magnitude indicates the degree of motor learning[3,4] and can be compared between unimanual and bimanual trials.

Aftereffects of the same arm were significantly smaller for bimanual reaching than unimanual reaching (73.8 ± 18.0% (mean ± s.d.); $F_{1,7} = 13.18$, $P < 0.01$; **Fig. 1d**). This pattern was reversed if subjects had been trained on bimanual movements (unimanual compared to bimanual,



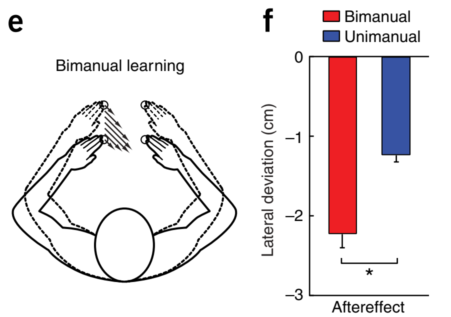


Figure 1 Partial transfer of learning across unimanual and bimanual movements. (**a**,**e**) Subjects learned to reach against a velocity-dependent force field that was applied to the left arm during either unimanual (**a**) or bimanual (**e**) reaching movements. Black arrows denote the approximate size and direction of the force field applied to the limbs during movement. (**b**) Left and right hand paths obtained during learning. The diagram shows the mean hand paths for baseline (that is, unloaded) reaching, initial and final hand trajectory when the load was applied, and aftereffects observed during catch trials. (**c**) Change in the lateral hand deviation at peak velocity; positive values indicate hand deviation to the right. The values are mean ± s.e.m. of each trial (learning and washout phases) and for each block consisting of 12 trials (learning phase with catch trials) across all subjects. (**d**,**f**) Summary of the aftereffects during catch trials for unimanual (**d**) and bimanual learning (**f**). There were significant differences in the lateral hand deviation between unimanual and bimanual aftereffects (*$P < 0.05$). Error bars indicate s.e.m.

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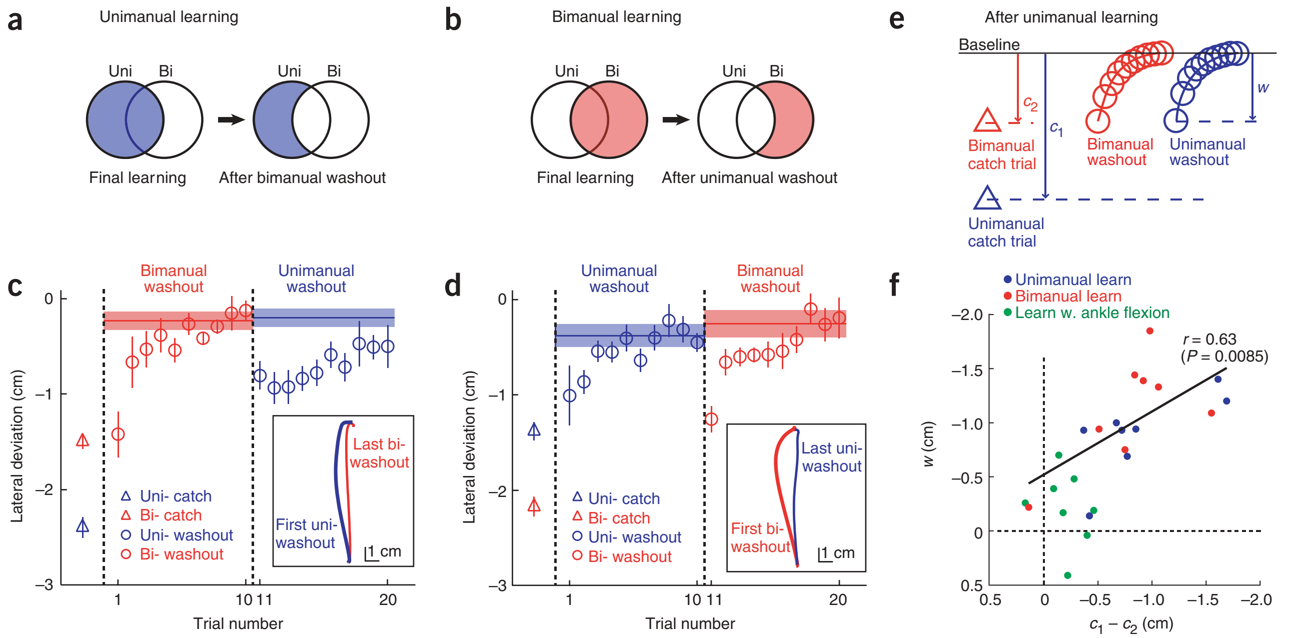

Figure 2 Effect of washout trials predicted from the partially overlapping neural control processes for unimanual and bimanual movements. (**a**,**b**) We predicted that bimanual washout trials after unimanual learning should not completely wash out unimanual learning (**a**), and vice versa (**b**). (**c**,**d**) Trial-by-trial change in the lateral hand deviation during washout trials (mean ± s.e.m.). Averaged hand paths for the last trial of the first set and the first trial of the second set of washout trials are shown in the insets. Colored horizontal lines with bar denote mean ± s.e.m. for baseline trials. Before the washout trials, subjects either performed unimanual (**c**) or bimanual (**d**) learning with catch trials, as in Experiment 1 (shown in **Fig. 1**). (**e**) Quantitative prediction of the effect of bimanual washout after unimanual learning. (**f**) The relationship between the predicted ($c_1 - c_2$) and actual (w) lateral hand deviation for the first trial of the second set of washout trials. Regression line based on data for unimanual and bimanual learning.

58.9 ± 11.7%; $F_{1,7} = 45.45$, $P < 0.001$; **Fig. 1e**,**f**, and **Supplementary Note** and **Supplementary Figs. 2** and **3** online); hence, incomplete transfer reflects a change in intralimb control rather than an additional bimanual constraint. Even though there are known differences in motor learning for dominant and nondominant arms[5], we observed similar results with perturbations to the right arm (**Supplementary Note** and **Supplementary Fig. 4** online). Also, hand motion of the unloaded right limb was unaffected by the learning process (**Supplementary Note** and **Supplementary Fig. 5** online).

This experiment (Experiment 1) suggested that there is a partial, but not complete, overlap in control processes for unimanual and bimanual skills. This predicts that the unlearning of a force field is also context dependent. Whereas the repeated presentation of catch trials (3–10 in a row) normally eliminates force-field learning[3,4], we predicted incomplete washout if the learning and unlearning contexts differ due to incomplete overlap (**Fig. 2a**,**b**). In fact, our second experiment demonstrated that following unimanual training and bimanual washout, subjects immediately re-expressed a significant aftereffect when performing their first unimanual catch trial (versus baseline or final bimanual trial, $P < 0.001$ by t-test; **Fig. 2c**). Some of the unimanual learning remained intact (though 'invisible') until the proper probe trial, unimanual reaching, was re-performed. We obtained identical results when the training and washout contexts were reversed (versus baseline or final unimanual trial, $P < 0.001$ by t-test; **Fig. 2d**). Moreover, the difference in unimanual and bimanual aftereffects ($c_1 - c_2$ in **Fig. 2e**) successfully predicted the magnitude of residual learning (w in **Fig. 2e**; **Fig. 2f**).

In a control experiment, we confirmed that complete washout occurred if the training and initial washout were the same (**Supplementary Note** and **Supplementary Fig. 6** online). Catch trial effects and re-expressed aftereffects were much smaller if subjects learned the force field with their left arm while synchronously flexing their right ankle ($P < 0.01$ by t-test; green dots in **Fig. 2f**). Therefore, the magnitude of unimanual and bimanual interaction is specific to upper limb contexts; a gradient of interactions may reflect the somatotopic gradient of the motor system.

Our third experiment examined adaptation to conflicting force fields presented in alternation. Normally, this situation is extremely difficult to learn[6,7], but we predict that adaptation can occur simply by having one force field associated with unimanual movements and the other with bimanual movements.

This prediction was tested by exposing the subject's left arm to a rightward force field during unimanual movements and to a leftward force field during bimanual movements. Subjects exhibited significant learning between the early (trials 2–4) and late (trials 31–40) trials during this 'combined' task and significant aftereffects during catch trials (Holm's test, $P < 0.05$; **Fig. 3**). Subjects also exhibited a much slower washout than that normally observed, possibly reflecting the interaction of unimanual and bimanual washout trials. In contrast, when subjects reached with unimanual movements and the force direction was explicitly cued, they had no significant adaptation when the force fields were present (Holm's test, $P > 0.05$; **Fig. 3b–d**), and aftereffects were smaller for this 'unimanual-only' condition compared to the combined condition (Holm's test, $P < 0.05$; **Fig. 3e**, and **Supplementary Note** and **Supplementary Fig. 7** online).

It seems that behavioral context—unimanual versus bimanual—has a profound influence on learning and probably reflects differences in control processes for these two skills. Bimanual movements require substantive interhemispheric interactions[8,9] to coordinate movements of the two limbs, as well as greater involvement of cortical regions such

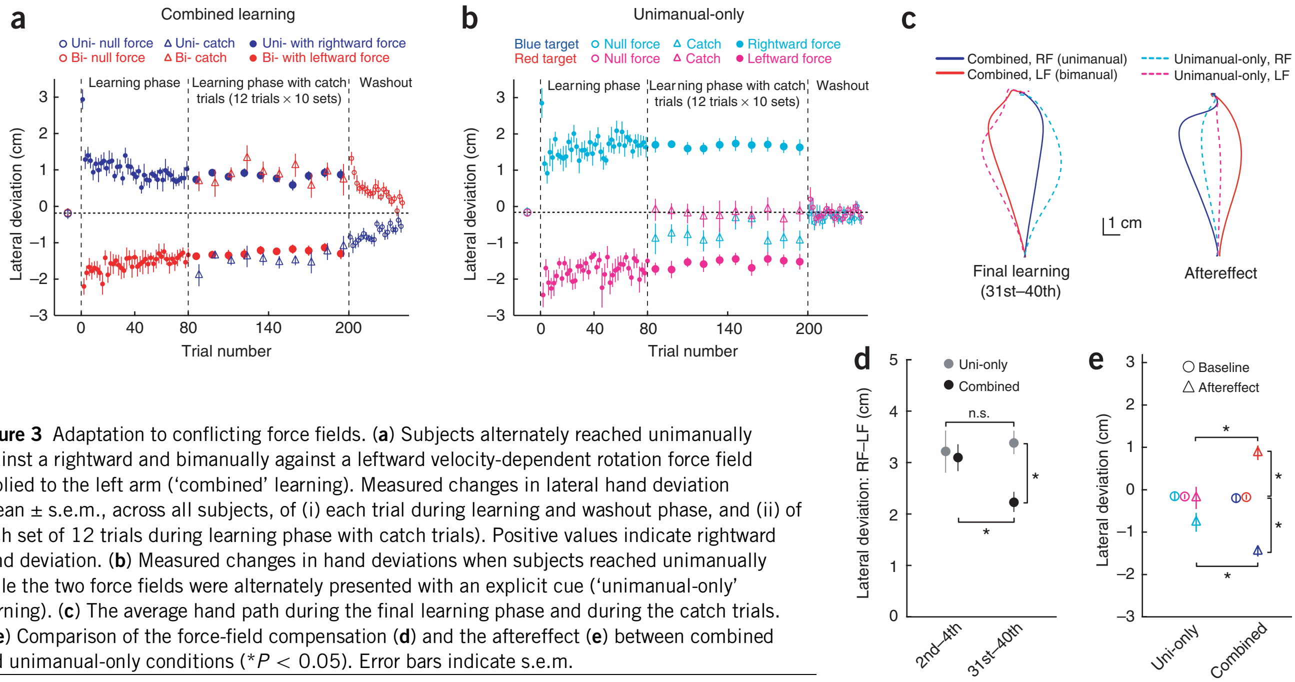

Figure 3 Adaptation to conflicting force fields. (**a**) Subjects alternately reached unimanually against a rightward and bimanually against a leftward velocity-dependent rotation force field applied to the left arm ('combined' learning). Measured changes in lateral hand deviation (mean ± s.e.m., across all subjects, of (i) each trial during learning and washout phase, and (ii) of each set of 12 trials during learning phase with catch trials). Positive values indicate rightward hand deviation. (**b**) Measured changes in hand deviations when subjects reached unimanually while the two force fields were alternately presented with an explicit cue ('unimanual-only' learning). (**c**) The average hand path during the final learning phase and during the catch trials. (**d**,**e**) Comparison of the force-field compensation (**d**) and the aftereffect (**e**) between combined and unimanual-only conditions (*$P < 0.05$). Error bars indicate s.e.m.

as the supplementary motor area[10], which we believe alters neural processing throughout the sensorimotor system. A partial, but not complete, overlap in load-related activity in primary motor cortex has been observed between posture and movement[11]. A similar shift in load-related processing in the neural circuitry between unimanual and bimanual contexts may underlie the present observations on learning.

The present results also illustrate the efficacy and limits on the transfer between unimanual and bimanual skills in sports and rehabilitation. Isolated practice with 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 but that full transfer may never be possible owing to constraints on how the brain controls unimanual and bimanual movements. Thus, maximal performance of complex multilimb skills necessarily requires practice of the task in its entirety. Correspondingly, rehabilitation may be facilitated by bimanual motor practice[12] but is likely to require further unimanual training to maximize motor recovery.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

This study was designed by all three authors. Data collection and data analysis were performed predominantly by D.N. All three authors contributed to the writing of the paper.

COMPETING INTERESTS STATEMENT

The authors declare competing financial interests (see the *Nature Neuroscience* website for details).

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1. Finch, M. *Triathlon Training* (Human Kinetics, Champaign, Illinois, 2004).
2. Scott, S.H. *J. Neurosci. Methods* **89**, 119–127 (1999).
3. Shadmehr, R. & Mussa-Ivaldi, F.A. *J. Neurosci.* **14**, 3208–3224 (1994).
4. Lackner, J.R. & Dizio, P. *J. Neurophysiol.* **72**, 299–313 (1994).
5. Bagesteiro, L.B. & Sainburg, R.L. *J. Neurophysiol.* **88**, 2408–2421 (2002).
6. Gandolfo, F., Mussa-Ivaldi, F.A. & Bizzi, E. *Proc. Natl. Acad. Sci. USA* **93**, 3843–3846 (1996).
7. Osu, R., Hirai, S., Yoshioka, T. & Kawato, M. *Nat. Neurosci.* **7**, 111–112 (2004).
8. Swinnen, S.P. *Nat. Rev. Neurosci.* **3**, 348–359 (2002).
9. Carson, R.G. *Brain Res. Brain Res. Rev.* **49**, 641–662 (2005).
10. Donchin, O. *et al. J. Neurophysiol.* **88**, 3498–3517 (2002).
11. Kurtzer, I., Herter, T.M. & Scott, S.H. *Nat. Neurosci.* **8**, 498–504 (2005).
12. Cunningham, C.L., Stoykov, M.E.P. & Walter, C.B. *Acta Psychol. (Amst.)* **110**, 321–337 (2002).