

A motor learning strategy reflects neural circuitry for limb control

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During motor skill acquisition, **the brain learns a mapping between intended limb motion and requisite muscular forces**. We propose that regions where sensory and motor representations overlap are crucial for motor learning. In primary motor cortex, for example, cells that modulate their activity for motor actions at a joint tend to receive input from that same portion of the periphery. We predict that this correspondence reflects a default strategy—a Bayesian prior—in which subjects tend to associate loads at a joint with motion at that joint (local sensorimotor association) when there is ambiguity regarding the nature of the load. As predicted, we found that in the presence of uncertainty, humans inappropriately generalized elbow loads as though they were based on elbow velocity. Generalization improved when we reduced uncertainty by decreasing coupling between elbow velocity and load during training. These results illustrate a key link between motor learning and the underlying neural circuitry.

A key feature of human motor function is the ability to adjust motor patterns to compensate for physical loads applied to the limb^{1–5}. In general, a physical load (L) can be described by:

$$L = f(x_i), \quad (1)$$

where x_i represents spatial and/or temporal variables. Learning to move with these loads can be viewed as the brain estimating this association (that is, forming an internal model of the load) in order to match intended limb motion to requisite changes in muscular activity⁶. Mathematically, this seems straightforward, but many variables of movement are highly correlated, particularly when training occurs under limited conditions. For example, motion of the hand, elbow and shoulder often have similar temporal patterns during movement toward a single target; thus a load that depends on one of these variables will also be temporally correlated with the others. Although context estimation has been recognized as an important feature of motor planning^{7,8}, **little is known about context estimation during learning**⁹ or about how a subject chooses among many variables to create an internal model for novel loads.

One factor that may influence learning strategies is an inherent coupling between sensory and motor representations in motor regions of the brain such as the primary motor cortex^{10–13}, cerebellar nuclei¹⁴ and red nucleus¹⁵. In particular, several studies have shown that neurons in primary motor cortex that modulate their activity for motor actions at a joint tend to receive input from that same portion of the periphery^{10,11}. Our hypothesis is that this inherent feature of motor circuitry influences skill acquisition and reflects a default strategy, or Bayesian prior¹⁶, which assumes that a load at a joint is related to motion at that joint. Such a strategy would capture two essential facts: that intrinsic viscosity and other mechanical properties at a given joint

arise predominantly from muscles spanning that joint and that there is a preponderance of homonymous spinal reflexes, such as the stretch reflex. This prior can be readily overcome, given broad experience with a novel load¹. We predict that in the presence of uncertainty, however, when many variables are highly correlated, novel loads applied to a given joint will be erroneously associated with motion at that joint. By first giving subjects novel loads during reaching movements to one target (training phase) and then testing their knowledge of the load during movements to a second target (generalization phase), we found evidence to support this feature of the motor system.

RESULTS

Subjects made planar movements while wearing a KINARM (kinesiological instrument for normal and altered reaching movements), a robotic device that can apply loads to individual joints (Fig. 1a). In experiment 1, subjects moved their hand out from a start position to a target, a movement that required the same magnitude of motion at the shoulder and elbow (30° shoulder flexion and elbow extension for movements to the target; 30° shoulder extension and elbow flexion for movements back to the start position; Fig. 1b and Methods), resulting in a high correlation between shoulder and elbow velocity ($r = -0.98$). After 20 unloaded movements, one of two loads was applied to the elbow during the training phase: a load proportional to elbow velocity (viscous load) or a load proportional to shoulder velocity (interaction load; Fig. 1c). In both cases, elbow extension was resisted such that hand paths were initially perturbed, but trajectory errors diminished with practice (Fig. 2a). Loads initially disturbed the natural coupling between elbow and shoulder motion, but this coupling gradually strengthened with practice (Fig. 2b).

After subjects had completed 40 movements with a given load in the training phase, we assessed their performance in a

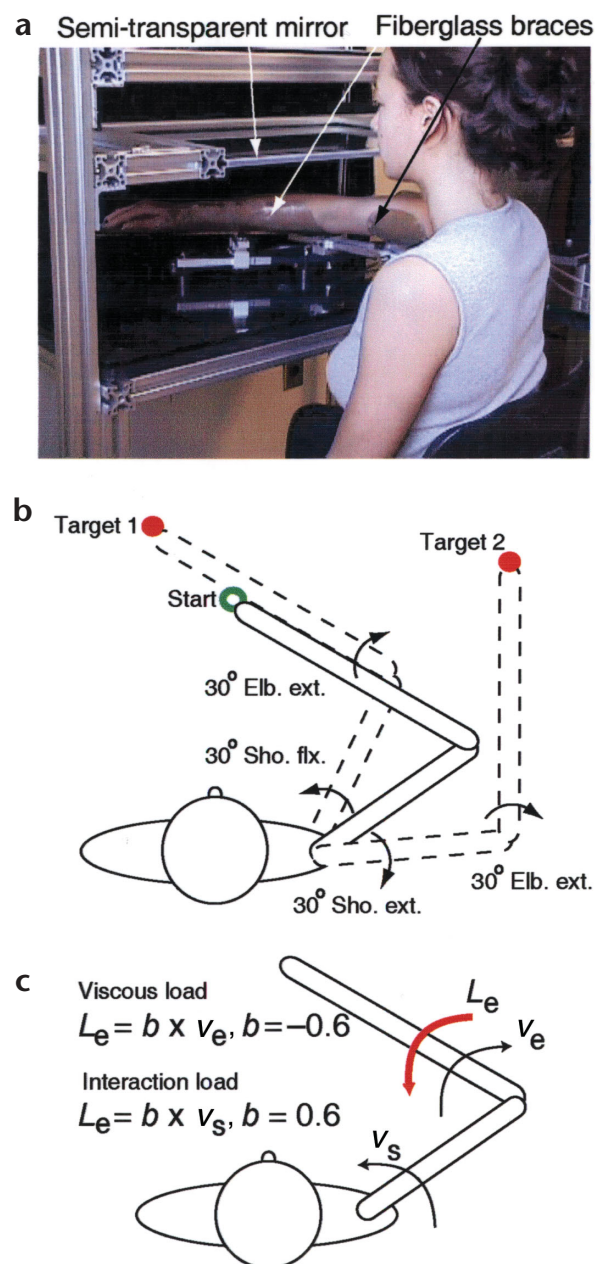


Fig. 1. The experimental apparatus, target locations and load types. (a) The KINARM is a mechanical, four-bar linkage with hinge joints that align with the centers of rotation of the shoulder and elbow to permit subjects to make reaching movements in the horizontal plane. Two torque motors attach to the linkage such that loads can be applied to each joint independently. (b) In experiment 1, subjects were required to move out and then back from a central start target and one of two peripheral goal targets, both requiring similar amounts of rotation at the two joints, but in opposite directions at the shoulder. (c) The magnitude of the viscous load applied to the elbow, L_e , was proportional ($b = -0.6$ Nm·s/rad) to the angular velocity of the elbow, v_e . The interaction load, L_e , was proportional ($b = 0.6$ Nm·s/rad) to the velocity of the shoulder, v_s .

generalization phase^{1,17}. We instructed subjects to make a single out-and-back movement to the generalization target and then five movements to the training target. This sequence was repeated until a total of five movements to the generalization target had been completed. We adopted this order of move-

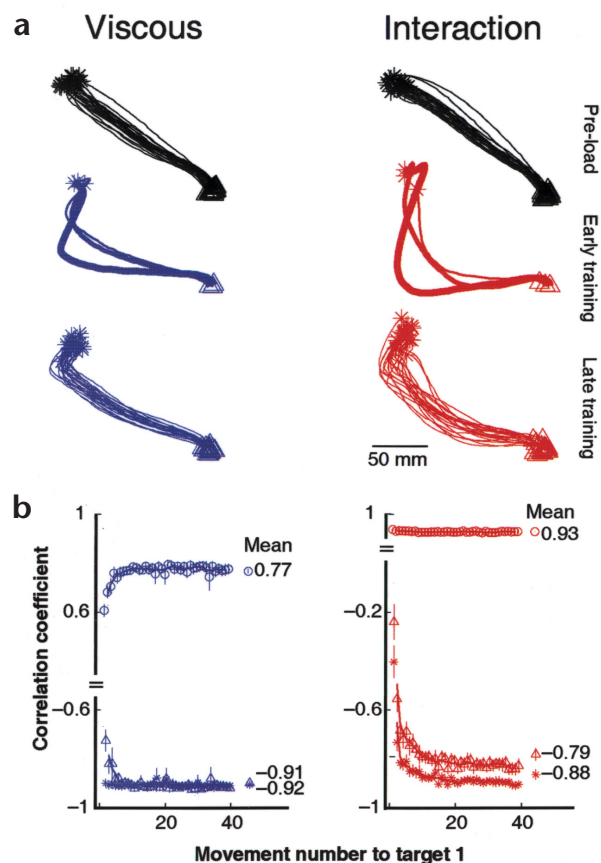


Fig. 2. Reaching movements to the training target with the viscous (left, blue) and interaction (right, red) loads. (a) Hand trajectories of a typical subject (Δ , hand position at movement onset; $*$, hand position at movement offset). Both sets of pre-load movements (black) are shown in the top panels. Middle panels show trials 1–3 of the training phase (loaded), with line thickness decreasing in that order. The final 20 loaded movements are shown in the bottom panel. (b) Correlation coefficients between shoulder velocity and elbow load ($r_{(vs, Le)}$; \circ), elbow velocity and elbow load ($r_{(ve, Le)}$; $*$) and shoulder velocity and elbow velocity ($r_{(vs, ve)}$; Δ) for each trial of the training phase of experiment 1 across all subjects (mean \pm s.e.m.). Solid lines represent a three-point moving average.

ments to minimize adaptation to the load in the generalization direction. These new movements reversed the shoulder–elbow coupling experienced during movements to the training target by requiring 30° extension at both joints (Fig. 1b). The viscous load resisted elbow motion to this target, whereas the interaction load assisted elbow motion. Subjects naturally generate movements with relatively consistent velocities that depend on task distance and accuracy requirements¹⁸. We measured initial elbow velocity (200 ms after movement onset) to assess whether subjects appropriately adjusted their motor patterns for the applied loads.

Movements to the generalization target with the viscous load were not significantly slower than unloaded baseline movements (84% of baseline movement elbow velocity, $P > 0.05$; Fig. 3a–c), but subjects moved significantly faster to the generalization target when the load was removed (129% of baseline movement elbow velocity, $P < 0.05$). This indicates that subjects learned and could generalize the viscous load, paralleling trajectory improvements during the training phase of the task.

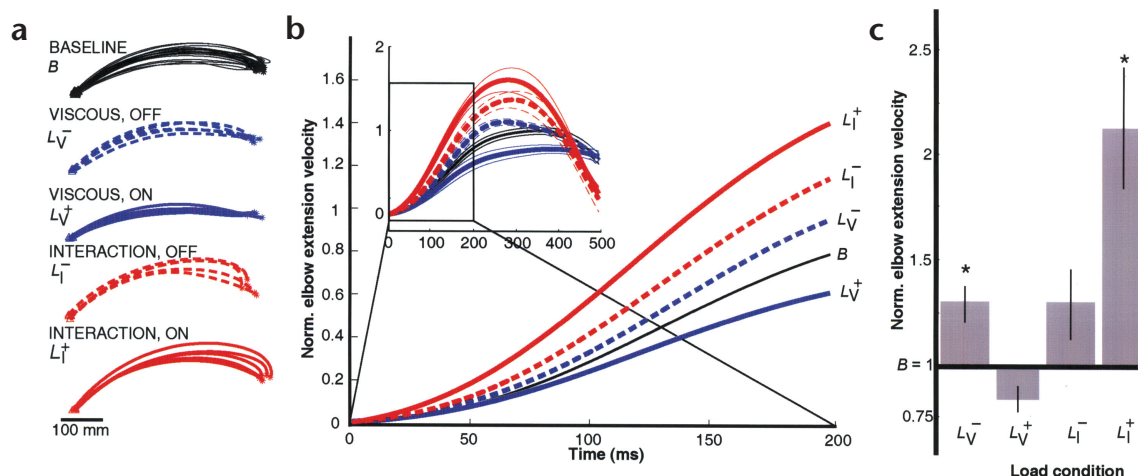


Fig. 3. Results from the generalization phase of experiment I. (a) Hand trajectories of a typical subject for movements to the generalization target all baseline movements, and movements for each load condition are shown, with symbols the same as those for Fig. 1a. (b) A typical subject's elbow extension velocities for movements to the generalization target in each load condition (mean \pm s.e.m., normalized to peak baseline velocity). Inset shows the first 500 ms of movement with the first 200 ms expanded in the main panel. Solid black, baseline (B); dash blue, viscous, off (L_V^-); solid blue, viscous, on (L_V^+); dash red, interaction, off (L_I^-); solid red, interaction, on (L_I^+). (c) Elbow velocities during movements to the generalization target at 200 ms, normalized to the baseline value, across all subjects in experiment I (mean \pm s.e.m.). Asterisks indicate a statistically significant result with $P < 0.05$ (t-test).

With the **interaction load**, by contrast, there were profound changes in movement speed to the generalization target (Fig. 3a–c); **subjects failed to scale both the load magnitude and sign**. Apparently, they assumed the load was viscous and thus resisted elbow motion to the generalization target. Elbow velocity 200 ms into the movement was roughly twice the speed observed during baseline reaching movements (213% of baseline movement elbow velocity, $P < 0.001$). Even when the interaction load was not applied to the generalization target, subjects still moved faster than expected, similar to the unloaded trials after training with the viscous load. **In effect, our subjects experienced a motor illusion and erroneously prepared for a resistive rather than assistive load.**

One possible explanation of the present results is that the motor system preferred symmetric impedances, that is, impedances that have equal off-diagonal terms. The interaction load used in the first experiment was non-symmetric, with a single term relating elbow load to shoulder motion. Therefore, we repeated the experiment with seven subjects using a symmetric interaction condition with loads at both the shoulder and elbow joints that were proportional to the velocity of the elbow and shoulder, respectively. Subjects trained with this load before making movements to the generalization target. Mean elbow velocities 200 ms into the movement were much faster than baseline (170%, $P < 0.005$). **Thus, even with symmetric loads, subjects still did not learn the appropriate association between joint motion and load.**

Another possibility is that subjects were learning the loads in endpoint rather than joint space. Our data, however, suggest that this was not the case. In the training phase, the loads at the elbow pushed the hand in a direction counter-clockwise to that of the intended movement. Thus, during the outward movements, the hand was pushed to the left (Fig. 2a), and during the movements back to the center, it was pushed to the right (data not shown). If subjects had learned this association, they would have expected a load that pushed their hand up during movements to the generalization target. Instead, subjects tended to have more upward hand trajectories for the no-load conditions as compared to base-

line (4.6 mm up from baseline, $P > 0.05$; Fig. 3a, for example). Furthermore, if subjects learned the loads in endpoint space, their elbow velocities should have been reduced rather than increased to create a more downward hand trajectory in the no-load conditions (Fig. 3c).

During the training phase, shoulder velocity and elbow load were highly correlated when interaction loads were applied in experiment 1 ($r_{(v_e, L_e)} = 0.93$), but elbow velocity and elbow load were also highly correlated ($r_{(v_s, L_e)} = -0.88$; Fig. 2b). **We suggest that this high correlation between elbow velocity and load created uncertainty regarding the nature of the load**, and subjects therefore used a default strategy of associating elbow load with elbow motion.

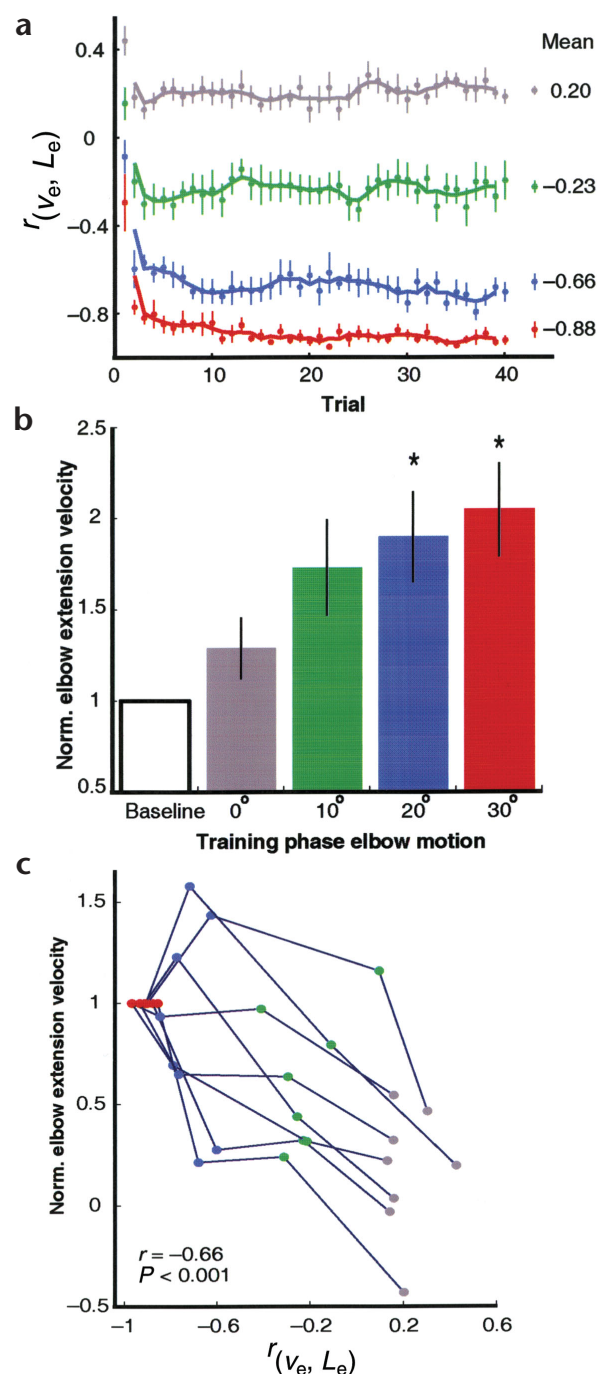
We performed a second experiment to assess **whether reducing load uncertainty improved generalization with interaction loads by decreasing the correlation between elbow velocity and elbow load during the training phase of the task**. In separate, randomly ordered blocks, subjects were trained with the interaction load for movements requiring 30° of shoulder flexion and either 30, 20, 10 or 0° of elbow extension. The magnitude and sign (that is, the flexor load to resist extension) of the load was constant across all four movement blocks, but the correlation between elbow velocity and elbow load decreased when movements to the training target required less elbow motion (Fig. 4a).

As the amount of elbow motion to the training target was reduced, initial elbow velocity during movement to the generalization target approached baseline (Fig. 4b). In other words, as elbow velocity and elbow load were uncoupled during the training phase, subjects began to learn the appropriate association (or internal model) between shoulder velocity and elbow load (Fig. 4c).

DISCUSSION

Our results suggest that **in the presence of uncertainty**, a default strategy is used to learn novel loads; **this strategy is to associate motor actions at a joint with sensory feedback from that same joint**. Although subjects always had sufficient information to identify the interaction load as one based on shoulder velocity, they misinterpreted the load as one based on elbow velocity





when there was a high correlation between elbow velocity and load during training. We posit that **this local association strategy for movement control reflects brain circuitry involving individual neurons that have overlapping sensory and motor representations.** This local association may even be advantageous for adapting to external forces, given that viscous or other loads applied at the hand tend to generate comparable loads in joint space. Such a learning strategy is consistent with, although not predicted by, previous observations that learning of novel endpoint loads tends to occur in intrinsic coordinates¹ and that the ability to generalize loads parallels the broad tuning of neurons in primary motor cortex¹⁷.

Fig. 4. Changes in elbow motion during training influences generalization of interaction loads. **(a)** Correlation coefficients between elbow velocity and elbow load ($r_{(v_e, L_e)}$) for each training movement to targets requiring 30° shoulder flexion and 0° (gray), 10° (green), 20° (cyan) or 30° (red) elbow extension (mean \pm s.e.m. across all subjects during experiment 2). Solid lines represent three-point moving averages. **(b)** Elbow extension velocities 200 ms into the movement toward the generalization target after training to targets requiring different amounts of elbow motion (normalized to the baseline value). **(c)** Relationship between elbow velocity–elbow load correlation ($r_{(v_e, L_e)}$) and elbow velocity 200 ms into the movement toward the generalization target. Results are plotted for each subject ($n = 8$), where elbow velocity is scaled from 0 (baseline elbow velocity) to 1 (elbow velocity for target requiring 30° elbow extension).

A local association between sensory and motor representations may reflect an optimal strategy for motor learning akin to strategies for perceptual estimation^{19,20}. Specifically, it has been suggested that motion illusions reflect an optimal percept assuming sensory noise (uncertainty) and a default strategy of assuming slow motion, a prior in Bayesian statistics¹⁶. The fact that time-varying force fields are approximated as being state-dependent suggests that such Bayesian priors may also be used by the motor system during learning⁹. **We propose that the observed local association between motion and load at a joint may be an optimal default strategy for motor learning and adaptation, and, as a consequence, that this optimal strategy is reflected in the underlying motor circuitry.**²¹ Variations in a one-to-one mapping between sensory and motor representations would be expected when it is behaviorally relevant (and optimal). For example, there is an apparent increase in the number of proximal limb-related neurons in motor cortex responding to cutaneous input to the paw of quadrupeds (such as cats²²) as compared to primates¹².

The present data are defined in a relative joint–angle coordinate frame. This framework (over absolute joint angles or other engineering-inspired coordinate frames) was chosen because it most closely reflects the predominance of mono-articular muscles spanning the shoulder and elbow joints²³. The present results could also reflect a muscle-based strategy that would consider that some muscles, such as biceps, span both the shoulder and elbow. Further experiments are required to adequately separate which representation is most appropriate.

Although our results suggest that **the brain tends to associate motor action with sensory motion at a given joint, the sensorimotor system is certainly capable of learning more complex mechanical relationships, such as intersegmental dynamics during multi-joint movements.**^{24,25} The present experiment simply suggests that such complexities can be learned when they are disambiguated from the simpler relationship between joint motion and load. It is interesting to note that patients with cerebellar damage have difficulty compensating for intersegmental dynamics, and this may reflect an inability to deviate from the default strategy of a local association between sensory signals and motor action at each joint²⁶.

METHODS

Subjects. Twenty-one normal, healthy, right-handed volunteers (aged 20–48, 12 male, 9 female) gave written informed consent to participate in this study. Sixteen participated in experiment 1, and eight in experiment 2 (three took part in both experiments). The experiments were performed in accordance with the regulations of the Queen's University Research Ethics Board. The subjects were naive with respect to the goals of the experiment and had not previously experienced the loads applied by our apparatus.

Experimental device. The experimental setup and data acquisition were similar to our previous neural studies on non-human primates^{27,28}. Briefly, the human subjects performed reaching movements to visual targets while wearing a robotic exoskeleton called KINARM (Fig. 1a). Fiber-glass braces fixed to a fully adjustable linkage were attached to the right upper arm and forearm, permitting flexion and extension movements of the shoulder and elbow with the arm abducted into the horizontal plane. Two torque motors (Kollmorgen U12CBL, Radford, Virginia) attached to the linkage were capable of applying loads to each joint independently²⁸. Motor position, measured by resolvers attached to the motors, was converted to encoder-equivalent units and sent to a motor control card (mini-PMAC, Delta Tau, Chatsworth, California) in the host computer, which computed joint positions and velocities and controlled the magnitude of the torque applied by the motors. Target lights were presented in the plane of the task using an overhead projector and a screen positioned above a semi-transparent mirror^{3,27,28}.

Experiment 1. Trials were initiated with the index finger positioned at a central start target. This required shoulder and elbow angles of 35 and 115°, respectively, such that the hand was approximately in the middle of the workspace. One of two peripheral targets was used in each trial (Fig. 1b): target 1, the training target, required shoulder flexion and elbow extension of 30°; target 2, the generalization target, required 30° of extension at both joints. After maintaining their index finger at the start target for 1 ± 0.25 s, subjects moved as quickly and as accurately as possible to the goal target and maintained the finger at the target for 1 ± 0.25 s. The central start target then reappeared, and subjects returned to it in a similar manner to end the trial. Subjects had full vision of their hand and arm during all movements.

The experiment was broken down into four main phases: (i) a pre-load phase with unloaded reaches to target 1, (ii) a training phase with loaded movements to target 1, (iii) a generalization phase with movements to target 2 interspersed with five movements to target 1 and (iv) a post-load phase with unloaded movements to target 1. There were no discernible breaks between these blocks of movements.

Two types of mechanical loads were applied to the elbow joint (Fig. 1c). One, a viscous load (L_v), was applied to the elbow with a magnitude proportional to elbow angular velocity (v_e), such that $L_e = b \times v_e$, where $b = -0.6$ Nm/s/rad. The other, an interaction load (L_i), was also applied to the elbow but with a magnitude proportional to shoulder angular velocity (v_s), such that $L_e = b \times v_s$, where $b = 0.6$ Nm/s/rad. The loads were applied during both the movement to the goal target and the movement back to the start target.

Subjects were tested on two consecutive days; the viscous load (conditions 1 and 2) and the interaction load (conditions 3 and 4) were applied on separate days. Two conditions were tested each day. Either the load was applied during movements to both targets (conditions 1 and 3), or the load was applied during movements to the training target only (conditions 2 and 4). The order of the four conditions was balanced across all subjects. At the start of the first day, baseline movements to each target were collected for each subject during an experimental session in which no load was applied.

Experiment 2. The task was similar to experiment 1, except that movements to the training target required a different amount of elbow extension (0, 10, 20 or 30°) combined with 30° shoulder flexion.

Data analysis. Motor resolver position data were collected at approximately 300 Hz. Signals were re-sampled at 200 Hz and then filtered with a 6th order, zero-phase-shift Butterworth filter with an effective cut-off frequency of 8 Hz^{27,29}. Movement onset was determined by first identifying the time at which tangential hand velocity reached 30% of its peak, and then stepping back in time to the first velocity reversal, or 1 cm/s. Movement offset was defined as the last time hand tangential velocity exceeded 10% of its peak.

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Competing interests statement

The authors declare competing financial interests; see the Nature Neuroscience website (<http://www.nature.com/natureneuroscience>) for details.

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