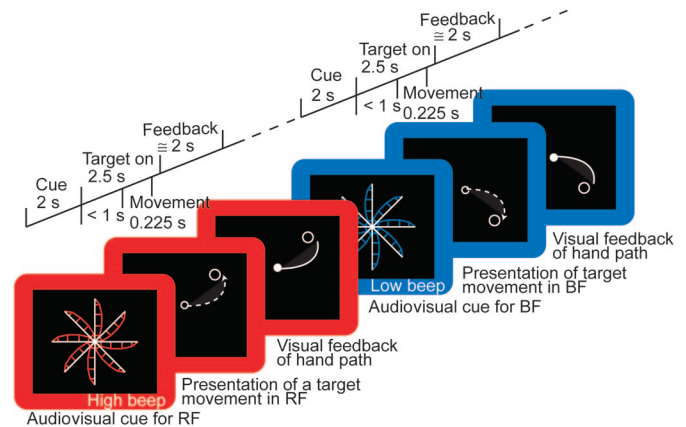


# Random presentation enables subjects to adapt to two opposing forces on the hand

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Studies have shown that humans cannot simultaneously learn opposing force fields or opposing visuomotor rotations, even when provided with arbitrary contextual information, probably because of interference in their working memory<sup>1–6</sup>. In contrast, we found that subjects can adapt to two opposing force fields when provided with contextual cues and can consolidate motor memories if random and frequent switching occurs. Because significant aftereffects were seen, this study suggests that multiple internal models can be acquired simultaneously during learning and predictively switched, depending only on contextual information.

Over two consecutive days, ten subjects learned reaching movements to eight targets located radially from a central start position. The movements took place in either a clockwise or a counterclockwise velocity-dependent rotational force field<sup>1,2,5</sup> (Fig. 1), presented in a random order. Each force field was repeated no more than 5 times (average, 1.76 times). This randomized sequence is different from previous studies in which two force fields were presented either in alternating blocks of many trials<sup>1</sup> or alternating trial by trial<sup>5,7</sup>. Before reaching in the clockwise force field (RF), subjects were presented with a red background, a red windmill-like diagram showing the direction and magnitude of rotational forces, and a high-frequency beep. Before reaching in the counterclockwise force field (BF), they were presented with a blue background, a blue windmill-like diagram and a low-frequency beep. After a 2-s presentation of these cues, one of the eight targets was randomly presented. Subjects were required to start within 1 s and reach the target within  $225 \pm 50$  ms (time between exiting the start circle and entering the target circle) with straight and uncorrected trajectories. The distance between the starting point and each target was 12.5 cm. Visual feedback of the hand position was suppressed during movements, but the entire hand path was shown after the movement terminated. One cycle consisted of 16 trials, including randomly ordered movements to all eight targets in the two force fields. On both days, the subjects executed a block of 14 cycles. On day 1, another block of 16 cycles was added, during which force fields were randomly (twice per cycle) turned off while audiovisual cues were retained, to examine aftereffects<sup>2</sup>. Before testing, subjects were familiarized with the task during a block of 192 trials without any force fields (null force field, NF; Fig. 2a).



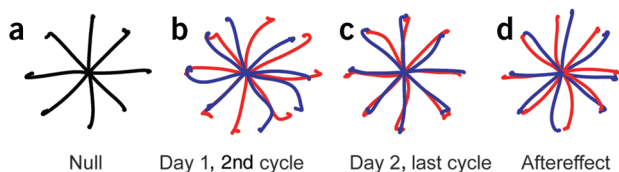
**Figure 1** Experimental procedure. See **Supplementary Note** online for details of force field (RF, BF) generation. ATR's ethics committee approved the experiments; subjects gave informed consent before participation.

During their initial exposure to the force fields, subjects' hand trajectories were highly distorted and curved in the direction of the applied force (Fig. 2b). However, as they practiced, the curvature of the trajectory decreased in both force fields (Fig. 2c). In the aftereffect trials, trajectory deviations were generally in the direction opposite to those registered initially (Fig. 2d), suggesting that subjects compensated for imposed dynamics in a predictive and feed-forward manner after 2 d of training.

Adaptation to each force field was quantified by the directional error, which is computed as the signed area between the actual hand path and the line joining the start and target centers, indicating the direction and amount of hand-path deviation from the straight line (deviation counterclockwise, +; clockwise, -). These directional errors were first averaged across 16 movements within two consecutive cycles for each force field and each subject, then averaged across subjects<sup>3,6</sup>. We compared the temporal evolution of these averaged directional errors in the two force fields (RF and BF) with those of the aftereffect trials (Fig. 3a). On day 1, subjects initially produced large negative (clockwise) errors in the RF and large positive (counterclockwise) errors in the BF. After 11–12 cycles, magnitudes of directional errors decreased, approaching those in the NF (black cross). When the same subjects were retested the next day, the initial directional errors were closer to those in the NF than those for early cycles on day 1, indicating retention of learning effects.

To confirm statistically significant learning and retention, we computed the difference errors under the RF and BF over cycles 2 and 3 as well as cycles 13 and 14 on the two days for each subject<sup>3,6</sup>. The difference error is defined as the difference in the directional errors between the RF and BF (BF - RF), and indicates the average area enclosed by hand paths in RF and BF. We averaged difference errors across all subjects (Fig. 3b). A significant difference was found across the four difference errors

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**Figure 2** Hand paths of a typical subject. (a) In the NF. (b) The second cycle on day 1. (c) Last cycle on day 2. (d) Aftereffects. Red, RF; blue, BF.

(ANOVA  $F_{3,36} = 4.46$ ;  $P = 0.0092$ ), and a *post-hoc* test showed that the difference error of cycles 2 and 3 on day 1 were significantly larger than the other three (Tukey's HSD test,  $P < 0.05$ ), supporting the idea that learning occurred. No significant differences were found between the difference errors of the last two cycles on day 1 and cycles 2 and 3 on day 2, supporting retention of motor memory.

For each force field, the direction of hand-path deviation in the aftereffect trials was opposite to that during learning (Fig. 3a). We compared directional errors in the NF, the RF aftereffects (NF with RF cues), and the BF aftereffects (NF with BF cues). Although the force field was the same in these three conditions, the directional errors were significantly different (ANOVA  $F_{2,27} = 13.58$ ;  $P < 0.0001$ ). The *post-hoc* test showed that the mean directional error was more counterclockwise for the RF aftereffect and more clockwise for the BF aftereffect, as compared to the NF (Tukey's HSD test,  $P < 0.05$ ).

Simultaneous learning under alternating blocked schedules<sup>1-4,6</sup> is possible if the orientation of the arm is altered between fields such that the mapping between motor commands and force changes and arbitrary visual or proprioceptive cues are ineffective<sup>1</sup>. Learning is very slow when two force fields are alternated trial by trial, even when cues are provided<sup>7</sup>. We evaluated whether richer contextual cues or random trial-by-trial switching contributed more to simultaneous learning. The difference error was significantly reduced after two learning days for six subjects who were given only the color background cue (*t*-test,  $P = 0.025$ ; Fig. 3c),

suggesting little contribution from the richer contextual cues. To determine whether randomness, rather than frequency, of cue changes is important, six other subjects were exposed to two force fields alternated trial by trial with the full audiovisual cues. The difference error was not significantly reduced after two learning days (*t*-test,  $P = 0.075$ ; Fig. 3d). No significant difference was seen for directional errors in the NF, the RF aftereffects or the BF aftereffects (ANOVA  $F_{2,15} = 1.68$ ;  $P = 0.2199$ ; Fig. 3e). Subjects did not adapt well to alternating, and therefore frequent, but predictable force-field changes. Based on a previous study<sup>1</sup> and our failure to find a significant difference in errors between consecutive trials when the same force field was repeated two or three times (ANOVA;  $P = 0.807$  for day 1,  $P = 0.832$  for day 2), it is unlikely that having several repetitions of the same force fields within the random schedule contributes to the learning. We conclude that the random order, which necessitates immediate feed-forward switching dependent on audiovisual cues, was mainly responsible for successful learning. Nevertheless, simultaneous learning was more difficult than separate learning<sup>2</sup>. Four subjects who learned the two force fields separately achieved an error level, after only 4 cycles, similar to that after 11–12 cycles in the main experiment.

By providing cues before movement, and by denying on-line visual feedback, we demonstrated that subjects can predictively switch between acquired motor programs. Simultaneous learning of two mutually conflicting tasks has been reported to be difficult<sup>3-6,8</sup> or very slow<sup>7,9</sup> or to involve subjects readapting<sup>9,10</sup> rather than switching predictively. Predictive switching has been demonstrated<sup>11</sup>, but not for multiple conflicting environments. With random-order presentation, humans can adapt to two conflicting environments not merely by using feedback control<sup>9,10</sup> or impedance control<sup>12,13</sup> but at least partly through simultaneous acquisition of multiple internal models and their predictive switching. The results support the MOSAIC model<sup>14</sup> (see discussion<sup>15</sup>), which proposed that many controllers are selected and learned while gated partly by contextual information.

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

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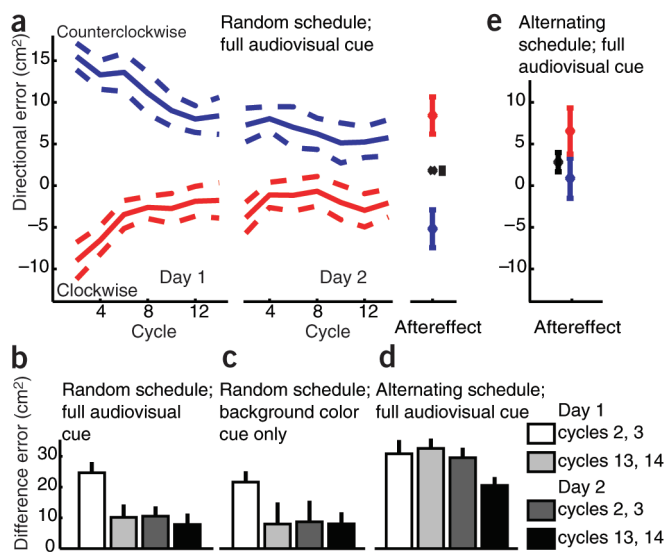
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**COMPETING INTERESTS STATEMENT**

The authors declare that they have no competing financial interests.

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**Figure 3** Learning curves. (a) Average directional errors and s.e.m. (dashed line) for RF (red) and BF (blue) averaged across two cycles, and aftereffect trials (red and blue) vs. NF (black) in the main experiment. The directional error for NF was positive as a result of the dynamics of the arm and PFM. Values averaged across all subjects. (b–d) Average difference errors across all subjects and s.e.m. for main experiment (b), task using only background color cue (c) and task using alternating schedule (d). (e) Average directional errors and s.e.m. for aftereffect trials (red and blue) vs. NF (black) in task using alternating schedule.

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