

# Large-scale citizen science reveals predictors of sensorimotor adaptation

Received: 27 January 2023

Accepted: 4 December 2023

Published online: 30 January 2024

 Check for updates

Jonathan S. Tsay<sup>1,7</sup>✉, Hrach Asmerian<sup>1,2,7</sup>✉, Laura T. Germine<sup>3,4</sup>,  
Jeremy Wilmer<sup>1,5</sup>, Richard B. Ivry<sup>2,6</sup> & Ken Nakayama<sup>2</sup>

Sensorimotor adaptation is essential for keeping our movements well calibrated in response to changes in the body and environment. For over a century, researchers have studied sensorimotor adaptation in laboratory settings that typically involve small sample sizes. While this approach has proved useful for characterizing different learning processes, laboratory studies are not well suited for exploring the myriad of factors that may modulate human performance. Here, using a citizen science website, we collected over 2,000 sessions of data on a visuomotor rotation task. This unique dataset has allowed us to replicate, reconcile and challenge classic findings in the learning and memory literature, as well as discover unappreciated demographic constraints associated with implicit and explicit processes that support sensorimotor adaptation. More generally, this study exemplifies how a large-scale exploratory approach can complement traditional hypothesis-driven laboratory research in advancing sensorimotor neuroscience.

Multiple learning processes contribute to successful goal-directed actions<sup>1</sup>. Among these processes, sensorimotor adaptation is of primary importance, helping ensure that our movements remain well calibrated in response to changes in bodily states and the environment. For example, sensorimotor adaptation can help a basketball player compensate for muscle fatigue or a bent rim<sup>1–3</sup>.

The study of sensorimotor adaptation traces back to the early days of experimental psychology<sup>4,5</sup>. George Stratton published his classic self-experiment in 1897, describing the behavioural and psychological changes he experienced when wearing mirror-inverting glasses for eight consecutive days. In the twenty-first century, these questions are typically addressed by using environments and virtual reality systems that allow the experimenter to perturb the movement feedback<sup>6–9</sup>. For example, a visuomotor perturbation can be introduced by rotating the position of the cursor from the actual hand position. The mismatch between the expected and actual positions of the visual feedback elicits adaptation—that is, movements in the opposite direction of the rotation that reduce and eventually nullify the visuomotor

error. If the perturbation is small, this change in hand angle emerges gradually and occurs outside the participant's awareness, a phenomenon known as implicit recalibration<sup>10</sup>. If the perturbation is large, the adaptive response may be accompanied by more explicit adjustments in aiming<sup>11–16</sup> (see ref. <sup>17</sup> for a review).

Studies of sensorimotor adaptation are typically conducted with specially designed apparatuses in controlled laboratory settings. This approach has been extremely successful in revealing critical spatial<sup>18–21</sup> and temporal<sup>22–26</sup> constraints on adaptation, as well as examining the contributions of different neural systems to this form of learning<sup>1,2,12,27–33</sup>. In-person research typically involves small samples<sup>34</sup>, increasing the likelihood that findings will fail to generalize outside the experimental context<sup>35–37</sup>. Moreover, studies of sensorimotor adaptation typically involve homogenous WEIRD samples (that is, Western, educated, industrialized, rich and democratic)<sup>34</sup>, with the expectation that motor learning would exhibit little variation across the human spectrum. This assumption, however, is challenged by recent studies revealing large individual differences in almost all psychological

<sup>1</sup>Department of Psychology, Carnegie Mellon University, Pittsburgh, PA, USA. <sup>2</sup>Department of Psychology, University of California, Berkeley, Berkeley, CA, USA. <sup>3</sup>Department of Psychiatry, Harvard Medical School, Boston, MA, USA. <sup>4</sup>Institute for Technology in Psychiatry, McLean Hospital, Belmont, MA, USA.

<sup>5</sup>Department of Psychology, Wellesley College, Wellesley, MA, USA. <sup>6</sup>Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, CA, USA. <sup>7</sup>These authors contributed equally: Jonathan S. Tsay, Hrach Asmerian. ✉e-mail: [xiaotsay2015@gmail.com](mailto:xiaotsay2015@gmail.com); [Hrach.Asmerian@berkeley.edu](mailto:Hrach.Asmerian@berkeley.edu)

**Table 1 | Summary of demographic and task features**

Feature	Category	Data
Age (yr)	–	26.3 (9–96)
Rating of clumsiness	–	0.0 (1.1)
Rating of enjoyment	–	0.3 (1.1)
Rating of video game frequency	–	-0.2 (1.4)
Amount of daily computer use (hours)	–	6.9 (3.2)
Amount of daily sleep (hours)	–	7.1 (1.4)
Baseline variability (°)	–	4.1 (2.0)
Baseline reaction time (ms)	–	289.8 (76.9)
Baseline movement time (ms)	–	182.4 (127.2)
Baseline search time (ms)	–	1,640.4 (338.6)
Screen size (pixels)	Height	787.3 (160.7)
	Width	1,525.8 (319.1)
Sex	Female	855
	Male	839
	Other	53
Handedness	Right	1,547
	Left	150
	Ambidextrous	50
Device	Mouse	764
	Trackpad	942
	Trackball	18
	Other	23
Racial origin	Multi-racial	79
	White	833
	Asian	431
	Latinx	116
	African American	55
	Native American	22
	Other	93
	Rather not say	113
Vision intact	Yes	1,584
	No	163
Neurological disorder	No	1,434
	Yes	313
Browser	Chrome	1,375
	Firefox	142
	Opera	42
	Safari	177
Target location	Cardinal	835
	Diagonal	912
Undergraduate major	STEM	695
	Psychology	208
	Social science	108
	Business	162
	Arts/humanities	201
	Other	373

**Table 1 (continued) | Summary of demographic and task features**

Feature	Category	Data
Highest level of education	Primary	21
	Middle	286
	Secondary	358
	Some college	388
	Technical school	54
	Bachelor	313
	Graduate	262
	Rather not say	54

The mean age (minimum to maximum) is provided. The means and standard deviations are provided for self-reported Likert ratings of clumsiness ('I am clumsy'), self-reported Likert ratings of overall experience completing the experiment ('I enjoyed the experiment') and self-reported Likert ratings of video gaming frequency ('I play a lot of video games'). A rating of -2 or 2 signified that the participant strongly disagreed or strongly agreed with the statement, respectively. The means and standard deviations are provided for baseline movement variability, reaction time, movement time, search time and screen size. The counts (that is, the number of participants) for each category are provided for the participants' sex, handedness, device used, racial origin, visual ability, neurological disorder, browser used, target location, undergraduate major and highest level of education achieved. ms, milliseconds.

processes, ranging from visual perception<sup>38</sup> to spatial reasoning<sup>39</sup>. If the goal of sensorimotor neuroscience centres on revealing human universals and understanding how individual experience gives rise to behavioural variability<sup>40–44</sup>, the time is ripe for a large-scale investigation asking how task and demographic features impact sensorimotor adaptation.

To address these issues, we designed a web-based visuomotor rotation task<sup>45,46</sup> and collected more than 2,000 sessions of data through a citizen science website ([www.testmybrain.org](http://www.testmybrain.org))<sup>47–50</sup>. This crowdsourcing approach enabled us to recruit a large, heterogeneous cohort of participants. Leveraging this unique dataset<sup>51</sup>, we built a cross-validated predictive model to identify core features of successful motor adaptation. The model not only identifies features that hold across the broader population but also highlights unappreciated features that modulate individual differences in motor learning. Gaining a deeper understanding of these individual differences could help instructors and clinicians tailor their interventions more effectively and inspire future hypothesis-driven laboratory studies to specify the computational mechanisms underlying this variability.

## Results

### The viability of studying motor adaptation outside the lab

We collected 2,121 sessions of data through the [testmybrain.org](http://www.testmybrain.org) website. The dataset included behavioural results from a web-based visuomotor rotation task along with answers to a demographic survey. Participants completed different numbers of sessions, and we employed a few variants of the task (Table 1, Supplementary Table 1 and Methods).

We first focused on naive participants who completed a task in which all reaches were to a single target (no. of sessions, 1,747). After a familiarization block with veridical feedback, a 45° visuomotor rotation was imposed between the participant's movement and visual cursor feedback (Fig. 1a). To compensate for this rotation, the participants exhibited significant changes in endpoint hand angle in the opposite direction of the rotation, gradually drawing the cursor closer to the target (Fig. 1b). Individuals exhibited changes in hand angle during both early (mean  $\pm$  s.e.m.,  $22.3^\circ \pm 0.3^\circ$ ) and late phases of adaptation (mean  $\pm$  s.e.m.,  $34.5^\circ \pm 0.3^\circ$ ) (Fig. 1d). When instructed to forgo the use of any strategy-based change in behaviour (for example, volitionally aiming away from the displayed target to offset the rotation) and reach directly to the target without visual feedback, the participants

exhibited robust aftereffects—a signature of implicit recalibration (mean  $\pm$  s.e.m.,  $12.6^\circ \pm 0.2^\circ$ ). Together, these data reveal a strong qualitative resemblance to those collected in person<sup>45,52</sup> (also see refs. 53,54).

A finer examination of the data from the early and late phases of the adaptation block revealed two subgroups of participants (Fig. 1d). Early in learning, a subset of the participants exhibited a rapid and large change in hand angle, whereas the other participants showed a gradual and modest change in hand angle ( $31.5^\circ$  versus  $10.0^\circ$ ; one-peak Bayesian information criterion (BIC),  $-342.3$ ; two-peak,  $-523.1$ ). These groups may reflect variation in how people learn. Participants in the second group may rely primarily on implicit recalibration, whereas those in the first group complement this process with an explicit aiming strategy to rapidly offset the effect of the large perturbation. This difference was also present late in learning, with some participants continuing to show only a modest change in hand angle ( $40.1^\circ$  versus  $14.3^\circ$ ; one-peak BIC,  $-177.7$ ; two-peak,  $-781.6$ ). Contrary to the early and late phases, there was only one subgroup in the aftereffect phase ( $12.6^\circ$ ; one-peak BIC,  $-1,422.7$ ; two-peak,  $-1,298.2$ ).

While the general features of the learning functions in our large online dataset are very similar to those found in data collected in the lab setting, early and late adaptation were lower<sup>52,55</sup>. As described in reviews of online studies, the dataset is likely to include individuals who are not attentive or fail to follow instructions<sup>56</sup>. With our dependent variables, reaching to the target rather than trying to make the cursor hit the target would result in attenuated learning. Differences in participant characteristics may also be relevant: unlike the typical WEIRD demography recruited in most laboratory experiments, our participant pool is notably heterogeneous, encompassing individuals with diverse characteristics such as advanced age and visual impairment. These features may have an attenuating effect on learning.

Baseline kinematic data were similar to those obtained in the lab (Fig. 1f–h)<sup>18,19,52</sup>. Reaction time, defined as the interval from target onset to when the cursor had moved 1 cm from the start position, was  $282.8 \pm 93.7$  ms online (median  $\pm$  semi-interquartile range (semi-IQR)). Movement time, defined as the interval from movement initiation (1 cm) to when the cursor reached the target amplitude (6 cm), was  $142.8 \pm 125.6$  ms (median  $\pm$  semi-IQR). Search time, the interval between movement termination and when the hand returned to the start position, was  $1,591.4 \pm 401.6$  ms (median  $\pm$  semi-IQR).

### Substantial individual differences throughout adaptation

There were substantial individual differences in hand angle across the three phases (Fig. 1d). Given the limited time available for each participant, we compared odd and even trials as an assessment of reliability. Split-half reliability was moderate to high across all three phases (Fig. 1e; correlation and two-tailed *t*-test: early,  $R^2 = 0.58$ ; 95% confidence interval (CI), (0.54, 0.60); Intraclass correlation coefficient, or ICC = 0.72;  $t_{1745} = 48.6$ ;  $P < 0.001$ ; late,  $R^2 = 0.86$ ; 95% CI, (0.85, 0.88); ICC = 0.93;  $t_{1745} = 103.6$ ;  $P < 0.001$ ; aftereffect,  $R^2 = 0.59$ ; 95% CI, (0.56, 0.62); ICC = 0.77;  $t_{1742} = 50.4$ ;  $P < 0.001$ ). These relatively strong effect sizes for the reliability measures are especially encouraging given that the participants performed the task without any supervision.

Our split-half approach, which involves comparing odd versus even trials, effectively measures internal reliability (for example, determining whether our sensorimotor learning task is unduly influenced by motor noise; Supplementary Fig. 1). This approach assumes that the two halves have similar variances but not that the two halves are temporally independent<sup>57,58</sup>. As such, this approach does not assess whether individual sensorimotor differences remain stable over time or across states (for example, it does not assess how performance might be influenced by changes in attentiveness). To address this, future research should adopt a test–retest approach by comparing learning performances across sessions. This approach can ascertain external reliability, ensuring that the observed sensorimotor differences are not merely artefacts of a single testing session. Nonetheless, it is crucial

to recognize that test–retest measures of reliability have their own limitations. Variation between sessions may not signal a lack of reliability in the selected task but could arise from individual differences in task-relevant features related to motor memory such as savings and interference<sup>59</sup> (for example, Fig. 2).

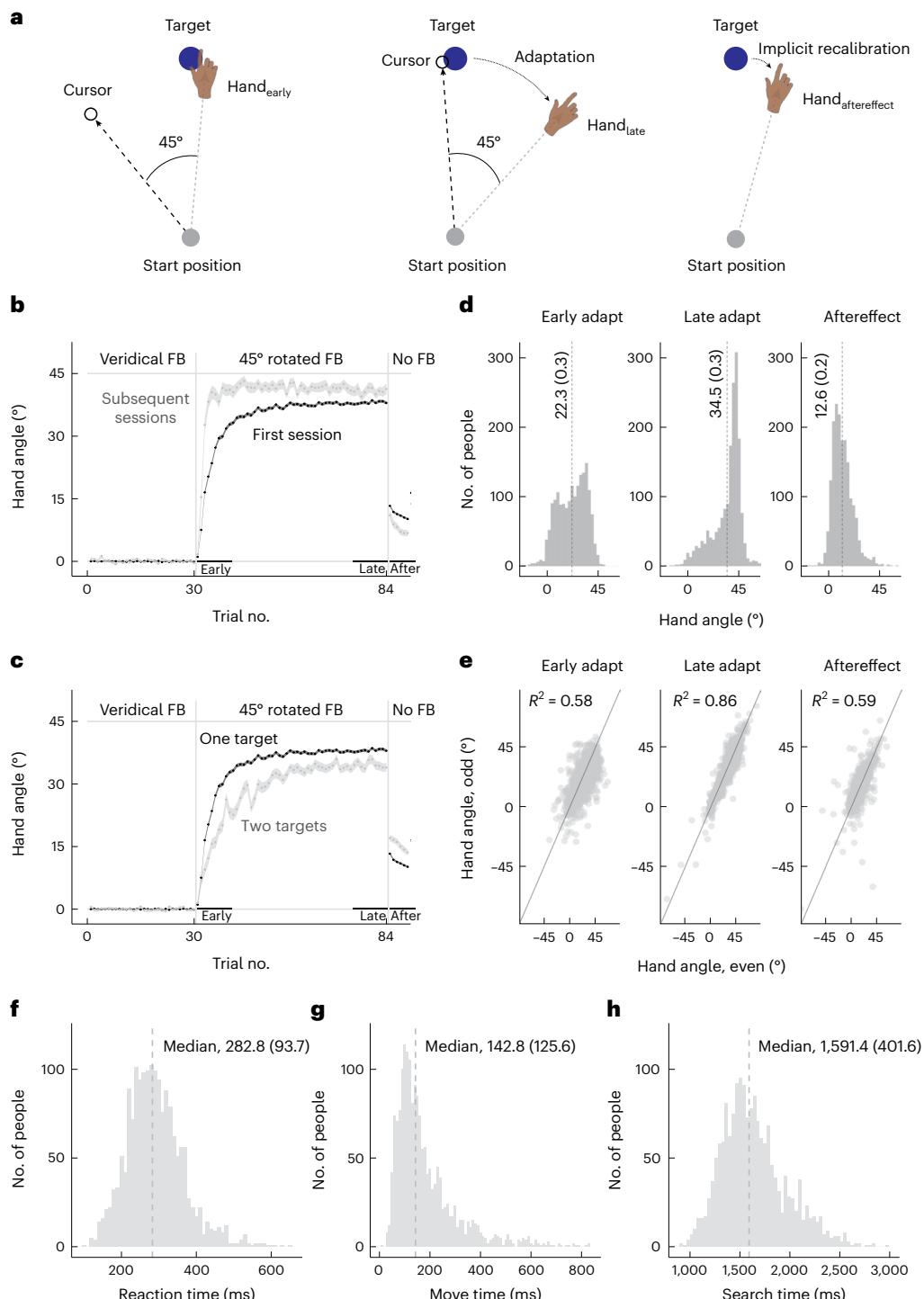
We next examined correlations in performance across the three phases (Extended Data Fig. 1). There was a moderate positive correlation in hand angle between the early and late phases (correlation and two-tailed *t*-test:  $R = 0.59$ ; 95% CI, (0.55, 0.62);  $t_{1745} = 30.2$ ;  $P_{bf} < 0.001$ ; Bonferroni-corrected for three comparisons). The correlation may reflect individual differences in the learning rates associated with implicit and explicit processes<sup>52</sup> (also see Supplementary Fig. 2). Another source of this correlation comes from the bimodal nature of performance (Fig. 1d): due to their failure to employ a strategy, non-learners would have low values for both phases, and, assuming some of the learners derive their strategy early on, these participants would have high values for both phases. Interestingly, there was no correlation between the early and aftereffect phases (correlation and two-tailed *t*-test:  $R = -0.01$ ; 95% CI, (-0.01, 0.04);  $t_{1744} = -0.4$ ;  $P_{bf} = 1$ ; Bonferroni-corrected for three comparisons) and only a weak correlation between the late and aftereffect phases (correlation and two-tailed *t*-test:  $R = 0.13$ ; 95% CI, (0.09, 0.18);  $t_{1744} = 5.7$ ;  $P_{bf} < 0.001$ ; Bonferroni-corrected for three comparisons). This pattern would be expected given that the aftereffect is dominated by the implicit component of learning whereas the early and late phases include for many participants a contribution from explicit strategy use. The degree of implicit recalibration will grow over the course of learning and, if approaching asymptote in the late phase, will dictate the level of the aftereffect.

### Re-examining classic findings in the sensorimotor literature

Prior studies have revealed an interesting dissociation for sensorimotor adaptation when participants repeat the task. Exposure to the same, large visuomotor rotation enhances the rate of adaptation, the classic signature of savings, but also results in an attenuation of the aftereffect<sup>59–64</sup>. The former is attributed to the recall of a successful re-aiming strategy<sup>63</sup>, whereas the mechanism for the latter remains an open question.

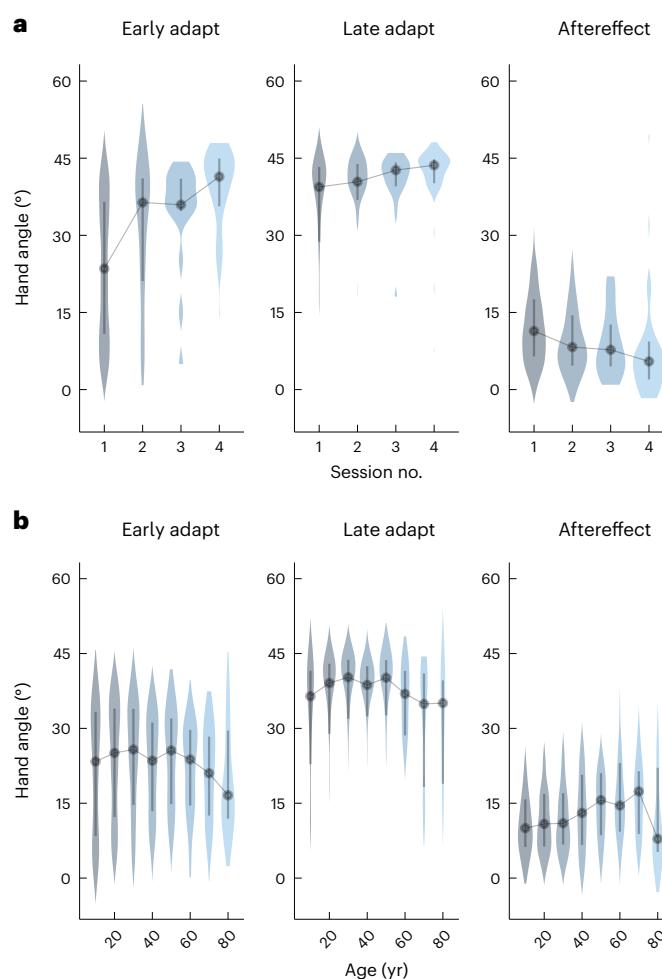
To quantify these effects in our data, we compared the learning functions between sessions for the participants who repeated the task on different days (Supplementary Table 1). Since our web-based approach makes it challenging to track which specific participants completed the experiment multiple times, we calculated savings in a between-participant manner. There was a significant phase  $\times$  session interaction (analysis of covariance:  $F_{6,5582} = 26.6$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.009$ ) (Figs. 1b and 2a): early adaptation and late adaptation increased across sessions (two-tailed *t*-test: slope of early adaptation,  $5.2^\circ$  per session; 95% CI, (4.0, 6.5);  $t_{5582} = 8.0$ ;  $P < 0.001$ ; slope of late adaptation:  $2.3^\circ$  per session; 95% CI, (0.98, 3.5);  $t_{5582} = 3.5$ ;  $P < 0.001$ ). However, the aftereffect was reduced (two-tailed *t*-test: slope of aftereffect,  $-1.5^\circ$  per session; 95% CI, (-2.7, -0.2);  $t_{5582} = 2.2$ ;  $P = 0.024$ ). Together, these data corroborate recent literature demonstrating the differential effects of repeated exposure on different learning processes<sup>59</sup> and expand on these findings by having some participants repeat the task up to four times.

This large dataset provides a unique opportunity to re-examine the influence of target quantity on motor adaptation<sup>52,65,66</sup>. Bond and Taylor<sup>52</sup> reported that reducing the number of targets amplified early adaptation and the size of the aftereffect. We failed to replicate this finding in our large dataset (Fig. 1c). In a comparison limited to naive participants (first session, Supplementary Table 1), we found a significant phase  $\times$  number of targets interaction (analysis of variance:  $F_{2,5777} = 23.5$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.008$ ). Compared with the one-target version, early and late adaptation were attenuated when there were two targets (post-hoc two-tailed *t*-test between versions: early, 95% CI,



**Fig. 1 | Web-based sensorimotor adaptation task and behaviour.** **a**, Schematic of the sensorimotor adaptation task. The cursor feedback (white circle) was rotated 45° with respect to the movement direction of the hand. The participants were instructed to move such that the cursor would intersect the target (blue circle). The left, middle and right panels display hand and cursor positions during the early, late and aftereffect phases of learning, respectively. **b**, Learning functions from naive participants who completed the one-target version of the task for the first time (black; no. of sessions, 1,747) versus non-naive participants completing the one-target version subsequent times (grey; no. of sessions, 157). The data are presented as median values  $\pm$  SEM. A hand angle of 0° denotes a movement directed to the target. FB, feedback. **c**, Learning functions for naive participants who completed the one-target (black;  $n = 1,747$ ) or two-target

version (grey;  $n = 181$ ) of the task. The data are presented as median values  $\pm$  SEM. **d**, Distributions of the participants' mean hand angles during the early, late and aftereffect phases. The dashed lines denote the median (IQR). **e**, Split-half reliability correlating hand angles on even and odd trials across all three phases (no. of sessions, 1,747; correlation and two-tailed  $t$ -test: early,  $R^2 = 0.58$ ; 95% CI, (0.54, 0.60); ICC = 0.72;  $t_{1745} = 48.6$ ;  $P < 0.001$ ; late,  $R^2 = 0.86$ ; 95% CI, (0.85, 0.88); ICC = 0.93;  $t_{1745} = 103.6$ ;  $P < 0.001$ ; aftereffect,  $R^2 = 0.59$ ; 95% CI, (0.56, 0.62); ICC = 0.77;  $t_{1742} = 50.4$ ;  $P < 0.001$ ). The grey dots denote individual participants; the grey lines represent the identity line. **f-h**, Distributions of the participants' mean baseline reaction times (**f**), baseline movement times (**g**) and baseline search times (**h**). The dashed lines denote the median (IQR).



**Fig. 2 | The effects of session and age on sensorimotor adaptation.** **a**, With re-exposure to the same visuomotor rotation across sessions (no. of sessions, 1,863; Supplementary Table 1), participants exhibit increased early and late adaptation across sessions but an attenuated aftereffect. **b**, The inverted-U effect of age (no. of sessions, 1,742). For ease of visualization, the participants' ages were binned on the basis of increments of 10: 107 individuals are closest to age 10, 1,068 to age 20, 269 to age 30, 126 to age 40, 61 to age 50, 59 to age 60, 24 to age 70 and 28 to age 80. In both panels, the width of each violin plot represents the data density, the dots indicate the median values and the vertical lines represent the IQR.

( $-7.3, -3.8$ );  $d = 0.13$ ;  $t_{5777} = 6.0$ ;  $P < 0.001$ ; late, 95% CI, ( $-3.7, -0.1$ );  $d = 0.05$ ;  $t_{5777} = 2.1$ ;  $P < 0.001$ ), but the aftereffect was enhanced (95% CI, ( $1.5, 5.1$ ));  $d = 0.08$ ;  $t_{5777} = 3.6$ ;  $P < 0.001$ ). This effect can be modelled by positing that implicit recalibration is composed of processes that operate at different timescales<sup>65,67–69</sup>. With one target, a process that learns and forgets quickly will accelerate learning but at a cost of overall retention. Alternatively, when reaches are limited to a single target, the discovery of an appropriate re-aiming strategy is probably facilitated. If explicit and implicit processes compete<sup>52,70</sup>, a corollary of this hypothesis is that implicit recalibration would be weakened.

This dataset also allows us to re-examine the effect of age on motor adaptation. Several studies have reported no effect of age<sup>71–73</sup>. Others have found that ageing impairs performance, especially late adaptation<sup>74–78</sup>, with the attenuation attributed to an age-related decline in strategy use. However, these studies have recruited modest sample sizes drawn from a limited age range<sup>71,79</sup> (except for refs. 74,80).

Here we revisited this 'age-old' question given that we tested participants ranging from 9 to 96 years old (Supplementary Table 1 and

Extended Data Fig. 2). Our analyses accounted for the influence of confounding variables, regressing out the influence of demographic variables correlated with age (Extended Data Fig. 3;  $|r| > 0.2$ : years of education,  $r = 0.46$ ; 95% CI, (0.42, 0.50);  $t_{1745} = 21.7$ ;  $P < 0.001$ ; video gaming experience,  $r = -0.28$ ; 95% CI, (-0.32, 0.24);  $t_{1745} = -12.4$ ;  $P < 0.001$ ). Age had a significant inverted-U effect on early adaptation (quadratic less than linear Akaike information criterion (AIC), -2.2; main effect of age in quadratic model:  $F_{1,1742} = 4.2$ ,  $P = 0.040$ ,  $\eta_p^2 = 0.004$ ; Fig. 2b) and late adaptation (quadratic less than linear AIC, -11.0; main effect of age in quadratic model:  $F_{1,1742} = 13.0$ ,  $P < 0.001$ ,  $\eta_p^2 = 0.01$ )—a pattern we attribute to changes in strategy use over the lifespan. Previous studies may have missed this pattern by sampling at different points along the inverted-U curve. Despite the drop in the magnitude of the aftereffect for the oldest group, the statistical analysis indicated that a linear model provided a better account of the effect of age on the aftereffect (linear less than quadratic AIC, -0.77; main effect of age in linear model:  $F_{1,1742} = 5.3$ ,  $P = 0.021$ ,  $\eta_p^2 = 0.01$ ), implying that the capacity for implicit recalibration may increase across the lifespan (also see ref. 81).

This pattern resembles that observed in Ruitenberg et al.<sup>80</sup>, in which the inverted-U effect was discernible during early and late adaptation. However, the two studies diverge in terms of the effect of age on the aftereffect. We attribute this to differences in the learning process indexed during the aftereffect phase: whereas visual feedback was provided in Ruitenberg et al.'s aftereffect phase (a manipulation that enables participants to de-adapt via strategic re-aiming<sup>82</sup>), no visual feedback was provided during the aftereffect phase in our study (a manipulation that allows us to index implicit recalibration in a pure manner).

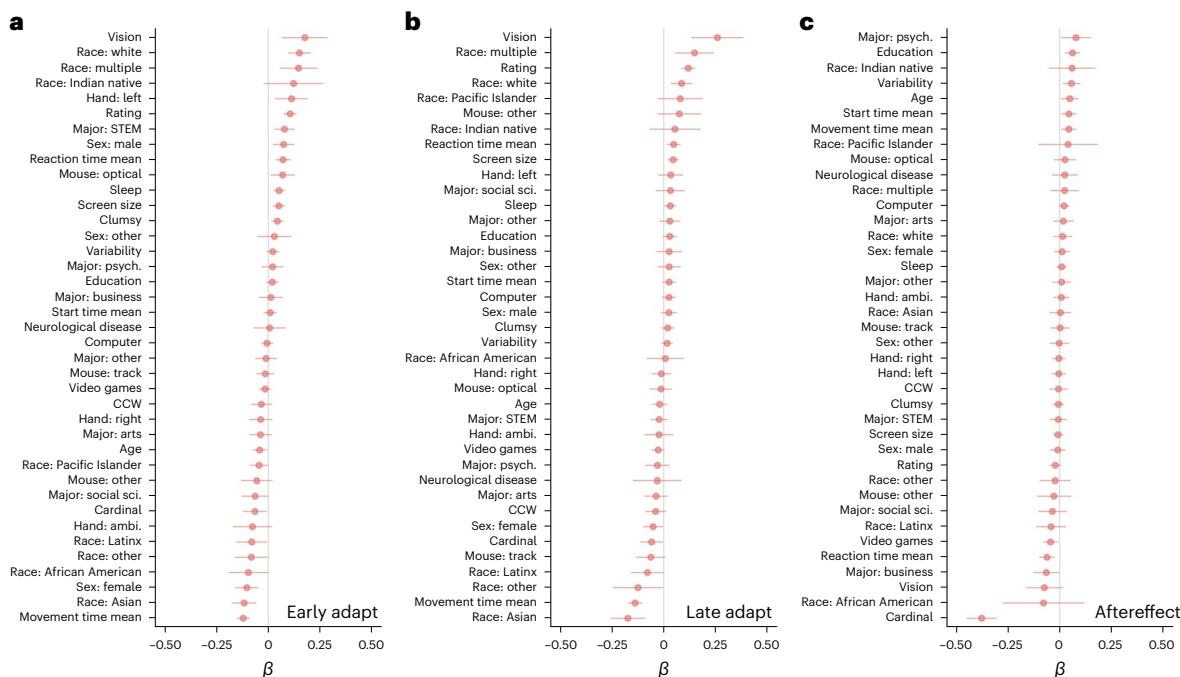
However, our results should be treated with caution for several reasons. First, the distribution of age groups was not balanced, with fewer participants at the extreme ends of the spectrum (Extended Data Fig. 2). Second, even though our study involved a highly heterogeneous sample, there may still exist some sample biases. For instance, our cohort may be more technologically proficient than the broader population, not to mention the limitation of participants primarily coming from English-speaking countries. To address these concerns, future studies are needed not only to recruit participants across age groups in a more balanced and uniform manner but also to strive for a more diverse sample.

### Identifying predictors of adaptation with machine learning

By collecting a range of demographic and kinematic variables in a large sample, we are positioned to identify predictors of sensorimotor adaptation and forecast sensorimotor behaviour that has not yet been observed<sup>35</sup>. To this end, we adopted a machine learning approach that segregated our sample of naive participants who completed the one-target version on their first session ( $n = 1,747$ ) into independent model training and testing subsets. *A priori*, we decided to build the model on 80% of the data and validate our model on the remaining 20%. We avoided overfitting by using a tenfold cross-validated approach with none of the data used for model training being used for model evaluation<sup>83</sup>. This conservative approach ensures that only variables that demonstrate predictive power are included in the model.

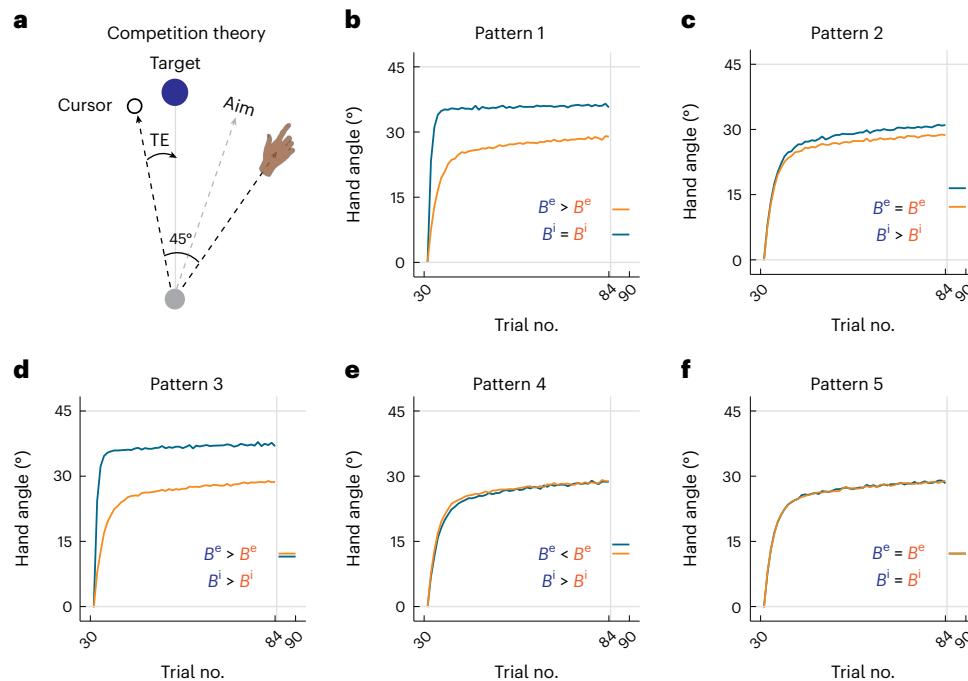
The best model accounted for 9.2% (3–17%), 7.8% (3–12%) and 11.6% (6–16%) of the variance in the early, late and aftereffect data, respectively (Extended Data Fig. 4). This model outperformed models built on randomly shuffled features (all  $P_{\text{perm}} < 0.001$ ) and varied minimally across different lasso hyperparameter settings (that is, the percentage of data used for training  $\times$  number of folds). These results not only highlight the robustness of our findings but also enable us to discover unappreciated features of motor adaptation in a powerful, exploratory fashion (Fig. 3).

We interpret the contributions of different features (Fig. 3) through the lens of the competition theory of adaptation (Fig. 4)<sup>84</sup>. This



**Fig. 3 | Features of the early adaptation, late adaptation and aftereffect phases.** **a–c**, Cross-validated regression coefficients ( $\beta$ ) indicate whether a feature positively or negatively predicts hand angle data during the early adaptation (a), late adaptation (b) or aftereffect (c) phase. The data are presented

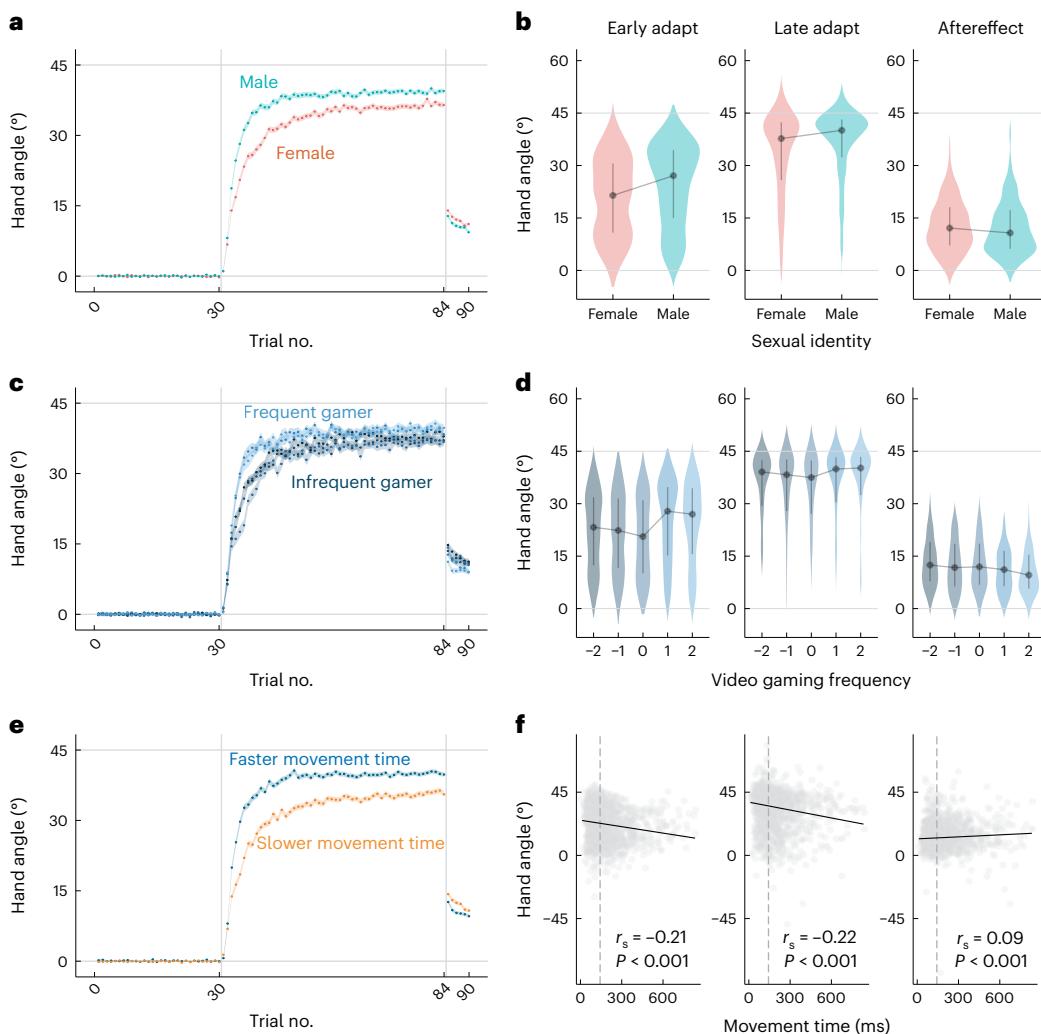
as mean values  $\pm$  95% CIs (bootstrapped by resampling the data 1,000 times). We used data from 1,747 sessions (naive participants who completed the one-target version of the task). CCW, counterclockwise.



**Fig. 4 | Five patterns of data simulated by the competition theory.** **a**, The theory posits that implicit and explicit processes are driven by a common task error, the mismatch between the cursor and the target. **b–f**, Model simulations with varying implicit ( $B^i$ ) and explicit learning rates ( $B^e$ ) produce five qualitatively distinct patterns of data.

theory states that total learning arises from the interplay of implicit and explicit processes. These two processes compete to reduce task error, the mismatch between the cursor and the target (see formalizations of the theory in Methods). Here we postulate that an individual's

features could impact the explicit learning rate, the implicit learning rate or both processes. Depending on what learning process is altered by an individual's characteristics, five qualitatively distinct patterns of performance can occur.



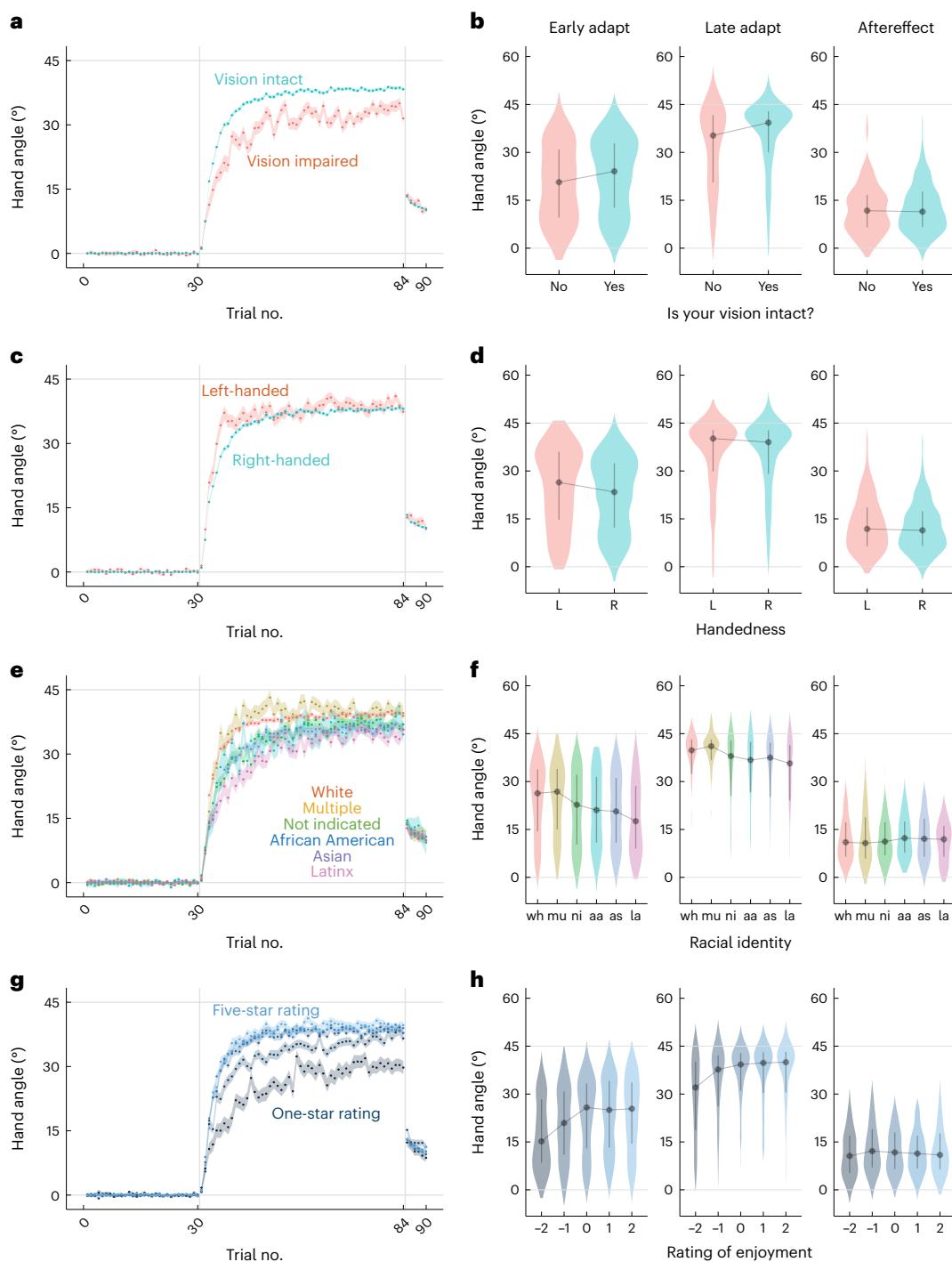
**Fig. 5 | Features corresponding to Pattern 1.** **a,b**, Sex. **c,d**, Ratings of video game frequency. **e,f**, Baseline movement times. In the left column, the data are presented as median values  $\pm$  SEM. In the right column, the width of each violin plot represents the data density, the dots indicate the median values and the

vertical lines represent the IQR.  $r_s$  denotes Spearman's correlation; the  $P$  values were obtained from two-tailed  $t$ -tests. We used data from 1,747 sessions (naive participants who completed the one-target version of the task).

Pattern 1 considers individual features that might enhance only the explicit learning rate but not the implicit learning rate. An increase in strategy use will accelerate learning (which involves the combined influence of explicit and implicit processes), leaving less of the error to be compensated for by implicit recalibration and thus resulting in an attenuated aftereffect (Fig. 4b). Features of the model that may be associated with the conjunction of higher adaptation and a lower aftereffect are sex, video gaming frequency and baseline movement time (Fig. 5). Whereas prior small- $n$  studies have yielded inconsistent results concerning the effect of sex on adaptation<sup>80,85</sup>, our dataset indicates that, compared with women, men adapt faster but exhibit a reduced aftereffect. Faster baseline movement times were also associated with faster adaptation but a lower aftereffect (the Spearman correlation is provided for all continuous features, as it is a measure relatively more robust to outliers<sup>86</sup>). It may be that participants who moved faster were more motivated to strategize<sup>87</sup>; alternatively, the strength of the error signal may weaken with movement time—an intriguing hypothesis that can be rigorously evaluated in the lab. Together, these features—in addition to repeated exposure to the perturbation (Fig. 1b) and target quantity (Fig. 1c)—appear to increase the propensity to use strategy, which indirectly reduces implicit recalibration via competition (even though implicit learning rates themselves are unaltered).

Pattern 2 considers individual features that might enhance only the implicit learning rate but not the explicit learning rate (Fig. 4c). An increase in implicit recalibration will enhance learning and the magnitude of the aftereffect. Interestingly, none of the features in the model modulate behaviour in a manner consistent with Pattern 2. Thus, none of the features selectively modulate the implicit learning process.

Pattern 3 considers individual features that might enhance both implicit and explicit learning rates at the same time. Concurrent increases in implicit and explicit learning rates can enhance overall learning; however, if the relative contribution of implicit learning remains constant, the aftereffect will remain invariant (Fig. 4d). A surprisingly large set of model features were associated with this pattern: visual ability, handedness, racial origin, ratings of enjoyment, baseline reaction time, average amount of sleep and screen size (Fig. 6 and Extended Data Fig. 5). Participants without visual impairment exhibited greater adaptation but had a similar aftereffect compared to those with visual impairment. This finding suggests that both strategic re-aiming and implicit recalibration may require high-fidelity visual input<sup>18,88–90</sup>. Moreover, participants who enjoyed the experiment exhibited greater performance. It may be that the reduced target error associated with greater adaptation caused the greater enjoyment. Alternatively, those who enjoyed doing the task may have been more willing to expend



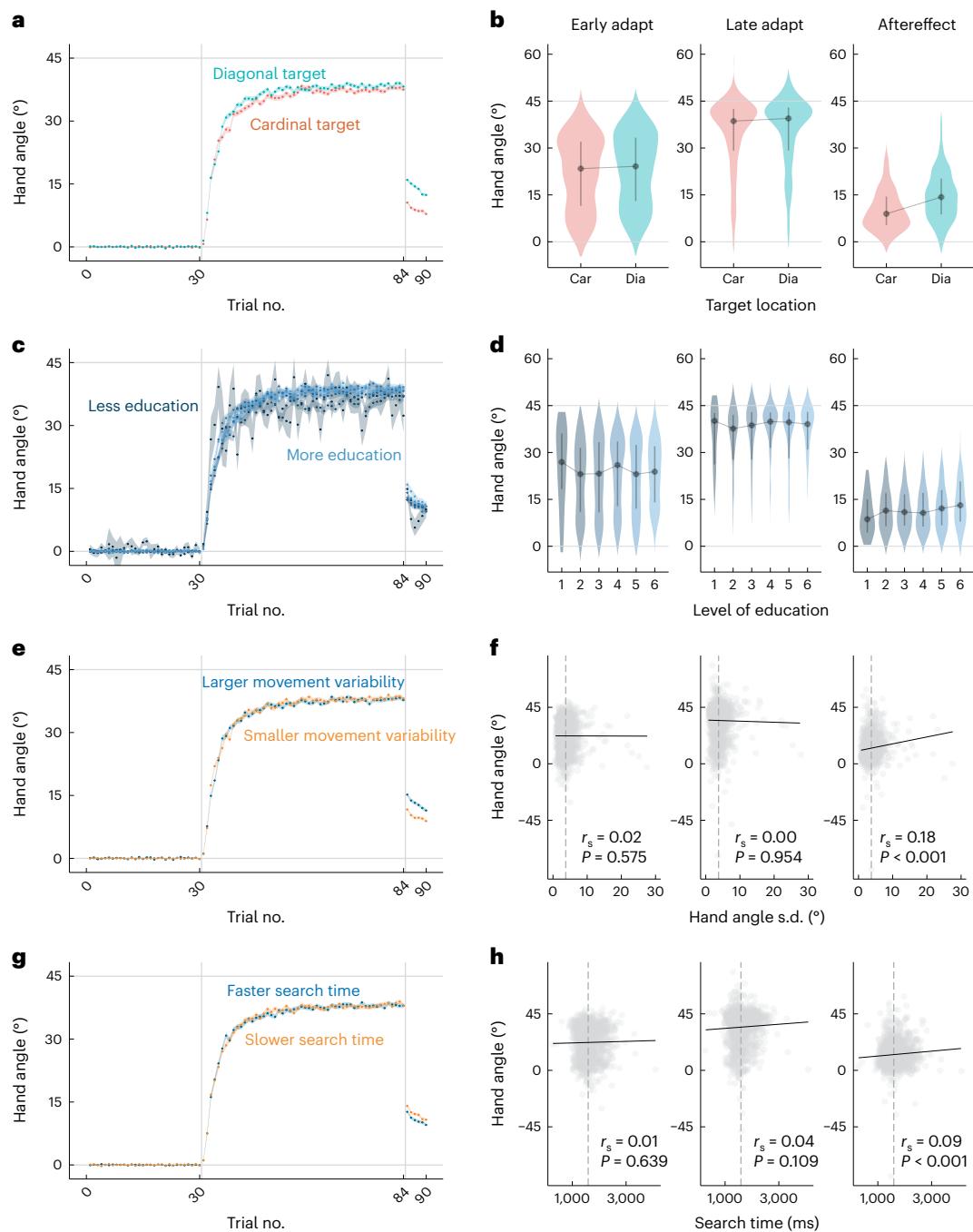
**Fig. 6 | Features corresponding to Pattern 3.** **a,b,** Visual ability. **c,d,** Handedness. **e,f,** Self-reported racial identity. **g,h,** Ratings of enjoyment of the experiment. In the left column, the data are presented as median values  $\pm$  SEM. In the right column, the width of the violin plot represents data density, the dots

indicate the median values and the vertical lines represent the IQR. We used data from 1,747 sessions (naive participants who completed the one-target version of the task).

effort to improve performance. Regarding the performance variables, strategy use is associated with longer reaction times<sup>91,92</sup>. This may account for the fact that slower baseline reaction times were associated with greater adaptation.

Pattern 4 considers individual features that might simultaneously enhance the implicit learning rate but attenuate the explicit learning rate. Opposing changes in implicit recalibration and explicit re-aiming can result in invariant overall learning. However, given that implicit

recalibration is enhanced, the magnitude of the aftereffect will increase (Fig. 4e). Features of the model associated with Pattern 4 are target location, baseline search times, baseline movement variability and level of education (Fig. 7). Participants reaching to diagonal target locations had an aftereffect that was almost twice as large as that observed for participants who reached towards cardinal targets. This result is especially noteworthy in that movement biases are known to vary across the workspace<sup>93–95</sup> yet are usually ignored in studies of sensorimotor



**Fig. 7 | Features corresponding to Pattern 4.** **a,b,** Target location. **c,d,** Highest level of education. **e,f,** Baseline movement variability. **g,h,** Baseline search time. In the right column, the width of each violin plot represents the data density, the dots indicate the median values and the vertical lines represent the IQR.  $r_s$  denotes Spearman's correlation; the  $P$  values were obtained from two-tailed

*t*-tests. In the left column, the data are presented as median values  $\pm$  SEM. We used data from 1,747 sessions (naive participants who completed the one-target version of the task). For the highest level of education, 1 indicates primary school, 2 indicates middle school, 3 indicates secondary school, 4 indicates technical school, 5 indicates undergraduate university and 6 indicates graduate school.

adaptation. Moreover, these results suggest that diagonal targets enhance implicit recalibration but attenuate strategy use compared with cardinal target locations.

Greater education was also associated with larger aftereffects. *A priori*, we expected that education would be associated with enhanced strategy use and thus impact early and perhaps late performance; we did not expect this variable to relate to implicit recalibration. However, years of education is collinear with age ( $r = 0.53, P < 0.001$ ), a feature observed to modulate the aftereffect. We hypothesize that it

is age and not education that is driving the increase in implicit adaptation (Fig. 2b)<sup>74,79,81,96,97</sup>. Future in-lab studies are required to tease these variables apart in a more controlled manner (for example, ref. 74).

The relationship of motor variability with implicit recalibration has been the subject of debate<sup>98,99</sup>. One perspective suggests that a more variable motor system is sensitized to correct for motor errors<sup>100,101</sup> and thus would be associated with greater motor adaptation. Alternatively, high variability may be considered a form of volatility, and this has been shown to drive down learning rates, at least in studies of reinforcement

learning<sup>99,102</sup>. It has also been reported that movement variability has no effect on recalibration<sup>99</sup>. Our results indicate that increases in baseline variability not only enhance the rate of implicit recalibration but also attenuate strategy use. It may be that increases in motor noise make it harder to evaluate a selected strategy.

Increases in the time required to return to the start position (that is, baseline search times) were also associated with larger aftereffects. Participants who are slow to find the start position may be those who are less kinaesthetically aware. Higher kinaesthetic variability has been shown to be associated with greater implicit recalibration<sup>60,103</sup>. Alternatively, longer search times may provide sufficient time for learning to consolidate<sup>104</sup> and therefore increase the extent of implicit recalibration. The longer search times would also afford participants more time to evaluate the effectiveness of a selected strategy.

Pattern 5 considers individual features that have no effect on implicit and explicit learning rates (Fig. 4f). Features in the model that modulate behaviour in a manner consistent with Pattern 5 include perturbation direction, device usage, self-reported neurological disease (Extended Data Figs. 6–8), browser type, undergraduate major, ratings of clumsiness and amount of daily computer usage. These results underscore how the extent of sensorimotor adaptation cannot be easily predicted by certain kinematic differences (for example, the use of trackpad or a mouse) or intellectual/sensorimotor experiences (for example, computer use).

We have highlighted how a large dataset not only is useful for establishing robust measures of sensorimotor learning but can also be used to explore a broad range of variables that impact performance. It is important to flag four major issues that qualify the inferences we can draw from this work. First, we opted to use competition theory as a framework to interpret the data. However, other theories offer different explanations for the observed patterns. One alternative is the independence theory<sup>12,55,105</sup>, positing that implicit and explicit processes are driven by distinct error signals: explicit strategy minimizes task error, while implicit recalibration reduces sensory prediction error (the difference between predicted and actual sensory feedback). The independence theory can provide an alternative interpretation of the observed patterns. Consider Pattern 1, in which there is an increase in the explicit learning rate only. Whereas the competition theory postulates that an explicit process siphons error away from an implicit process, independence theory attributes the attenuated aftereffect for high strategy users to variation in plan-based generalization<sup>93</sup>. Aiming further from the original target location will reduce the estimate of the aftereffect when measured at the target location.

Second, we recognize that the model's predictive capacity is modest, accounting for around 10% of the variance in the data. Moreover, the model incorporates correlated variables that pose statistical challenges in disentangling their interacting effects (Extended Data Fig. 3 and ref. 106). Despite these limitations, it is noteworthy that our model successfully captures some of the variance, including features that are typically ignored in studies of sensorimotor learning (for example, sex, target location and ratings of enjoyment).

Third, and relatedly, our findings indicate that most variables have relatively small effects on sensorimotor learning, collectively predicting a modest amount of variance in our held-out dataset. This result may be taken to indicate that none of the variables have a significant impact on sensorimotor learning. However, we hold a more optimistic perspective. This study provides one of the first big datasets for exploring the influence of multiple task and demographic variables on individual differences in sensorimotor learning; as such, the variables that survive cross-validation can be viewed as working hypotheses to help motivate future studies. Moreover, the small effects observed in simple visuomotor tasks (where individual differences may be limited) may compound to larger effects in complex motor learning settings (where individual differences are probably more pronounced).

Fourth, the model serves as an important benchmark in predicting, not simply explaining, individual differences in sensorimotor learning. Future studies can build on this approach, assaying a wider range of features, including those we might expect to be predictive of motor performance (for example, athleticism, musicality<sup>107</sup>, anatomical and functional variability in sensorimotor brain areas<sup>108–111</sup>, and gene expression<sup>112</sup>) as well as others we expect to be less predictive (for example, geographic location and socio-economic background). These additions would take us closer to a more accurate understanding of sensorimotor learning.

## Discussion

Our data-driven web-based approach offers a powerful method to study sensorimotor learning outside the traditional laboratory setting<sup>104,113–125</sup>. We have shown that these data are reliable and valid, reproducing as well as challenging classic findings in the literature. On the replication side, re-exposure to the same visuomotor rotation increased early and late adaptation<sup>62,63,67,126,127</sup> yet resulted in an attenuated aftereffect<sup>59</sup>. In contrast to previous findings<sup>52</sup>, increasing the number of targets attenuated late adaptation but, paradoxically, resulted in an enhanced aftereffect.

The large sample sizes possible in web-based studies offer a way to examine inconsistencies in the sensorimotor learning literature. For example, we expect it would be difficult to detect the effects of age in lab-based studies with small sample sizes. Our results point to a subtle inverted-U effect of age, with early/late adaptation peaking between 35 and 45 years old. Future in-lab studies can home in on the mechanisms underlying this non-monotonic function, asking how age-related cognitive decline may disrupt strategic re-aiming and how age-related neural degeneration may impact implicit recalibration.

Our web-based approach allowed us to tackle questions typically inaccessible to the lab and discover new predictors of sensorimotor adaptation. Leveraging this large dataset and a machine learning approach, we found that sex and movement time had selective effects on strategic re-aiming (Pattern 1). Interestingly, none of the features evaluated had a selective effect on implicit recalibration (Pattern 2). Other features impacted both processes. Impairments in vision, handedness, racial origin, ratings of enjoyment, baseline reaction time, average amount of sleep and screen size exerted unidirectional influences on implicit/explicit processes (Pattern 3), whereas target location, baseline search times, baseline movement variability and level of education modulated these processes in opposite directions (Pattern 4). Future studies can ask whether similar patterns are observed when tested with psychophysical methods that isolate implicit and explicit learning processes<sup>25,128,129</sup>.

There are notable limitations with this data-driven approach. Our predictive model explained only a modest amount of variance in the data. This may be due to the noisiness inherent in online data collection. In the future, we propose a few ways to reduce noise. First, studies could include more attention/comprehension checks to ensure that the participants fully understand the task instructions. There are also efforts to gamify web-based sensorimotor tasks, an approach that should enhance participants' attention and yield higher-quality data (for example, refs. 113,130,131). Second, studies could use a semi-supervised approach (such as video conferencing) to ensure that participants remain attentive throughout the experiment (for example, refs. 30,132,133).

Importantly, our predictive model is grounded in observational, correlational and often collinear data, making it difficult to make strong inferences about causality. In addition, there may be unmeasured confounds, many of which could affect our interpretation of the data (for example, internet speed, socio-economic status and type of occupation may modulate learning instead of racial origin, per se). Nonetheless, this exploratory approach provides a blueprint for future hypothesis-driven research aimed to meticulously tease apart different

theoretical accounts and effectively control for potential confounding variables. Exploratory and hypothesis-driven approaches can be used in a complementary manner to advance our understanding of sensorimotor neuroscience.

## Methods

### Inclusions and ethics

All participants provided their informed consent in accordance with policies approved by the Institutional Review Board at the University of California, Berkeley (Committee for Protection of Human Subjects: 2016-02-8439). Our participants were volunteers who visited [testmybrain.org](https://testmybrain.org), a citizen science website that allows people to participate in research studies in exchange for individualized feedback on their performance after each study.

### Statistics and reproducibility

Participants were recruited between 2019 and 2022 on a citizen science website ([testmybrain.org](https://testmybrain.org)) that provides personalized performance feedback in exchange for study participation. A total of 2,289 experimental sessions were collected. We excluded 168 sessions with erratic movements (that is, the standard deviation of hand angle exceeded 25°, or more than 20% of outlier data points were removed; see ‘Data analysis’) or systematic movements in the wrong direction (that is, mean heading angle was less than 0° or exceeded 75°), leaving 2,121 eligible sessions. Note that no statistical method was used to predetermine sample size. The participants were unaware of the experiment’s objectives, and no blinding procedures were implemented for the experimenters.

For the model-based analysis, we limited the data to participants who completed the one-target version of the task on their first session ( $n = 1,747$ ). This criterion excluded 374 sessions (Supplementary Table 1) in which there may have been confounds (for example, the two-target version impacted learning at all phases) and possible within-participant effects on behaviour (for example, savings or interference<sup>59</sup>). A summary of demographic and task features is provided in Table 1. A cross-correlation matrix of features is provided in Extended Data Fig. 3.

### Web-based sensorimotor adaptation task

All participants used their own laptop or desktop computer to access the [testmybrain.org](https://testmybrain.org) webpage that hosted the experiment (see a demo of the task at [https://multicclamp-c2.web.app/](https://multiclamp-c2.web.app/)). The participants made reaching movements by moving the computer cursor with their mouse or trackpad. The size and position of stimuli were scaled on the basis of each participant’s screen size. For ease of exposition, the stimulus parameters reported below are for a typical monitor size of 13 inches (1,366 × 768 pixels), and the procedure reported below is for the one-target version of the task.

On each trial, the participants made a centre-out planar movement from the centre of the workspace to a peripheral target. The centre position was indicated by a white annulus 0.5 cm in diameter, and the target location was indicated by a blue circle that was also 0.5 cm in diameter. The radial distance of the target from the start location was 6 cm. For each participant, the target always appeared at the same location on every trial. Each individual was randomly assigned a single target location selected from a set of eight possible locations (cardinal targets: 0°, 90°, 180° and 270°; diagonal targets: 45°, 135°, 225° and 315°).

To initiate each trial, the participant moved the cursor, represented by a white dot on their screen, into the start location. During an introductory phase, feedback was provided only when the cursor was within 2 cm of the start circle. Once the participant maintained the cursor in the start position for 500 ms, the target appeared. The participant was instructed to reach to the target using the cursor. If the movement was not completed within 500 ms, the message ‘too slow’

was displayed in red 20-point Times New Roman font at the centre of the screen for 750 ms.

During the experimental phase, visual feedback could take one of the following forms: veridical feedback, rotated feedback and no feedback. During veridical-feedback trials, the movement direction of the cursor was veridical with respect to the movement direction of the hand up to the target distance (6 cm). Once this distance was reached, the cursor position was frozen for 50 ms, and then the cursor disappeared. During rotated-feedback trials, the cursor moved at a 45° angular offset relative to the position of the hand up to the target distance (6 cm) before freezing for 50 ms. During no-feedback trials, the feedback cursor was extinguished as soon as the hand left the start circle and remained off for the entire movement. During the search phase after each movement, the veridical cursor was visible upon moving within 2 cm of the start circle.

Given the access demands for the [testmybrain.org](https://testmybrain.org) website, we were limited to only about 10 min of data collection. The participants therefore completed three blocks of trials (90 total trials): a baseline veridical-feedback block (30 trials), a rotated-feedback block (54 trials) and a no-feedback block (6 trials). During the rotation block, the direction of rotation (that is, clockwise or counterclockwise) was counterbalanced across participants.

### Attention and instruction checks

It is difficult in online studies to verify that participants fully attend to the task. To address this issue, we sporadically instructed the participants to make specific key presses: ‘Press the letter ‘b’ to proceed.’ If participants did not press the correct key, the experiment was terminated. These attention checks were randomly introduced within the first 20 trials of the experiment. We also wanted to verify that the participants understood the goal of the task. To this end, we included one instruction check: ‘Identify the correct statement. Press ‘a’: I will identify the movement that brings the white dot to the target. Press ‘b’: I will keep reaching directly towards the target location.’ The experiment was terminated if participants did not press the correct key (that is, press ‘a’).

### Data analysis

The primary dependent variable was hand angle, defined as the angle of the hand relative to the target when the amplitude of the movement reached the target radius (6 cm). Positive hand angle values correspond to the direction opposite the rotated feedback (that is, we flipped all hand angle values where a counterclockwise rotation was provided). Reaction time was defined as the time to move 1 cm. Movement time was defined as the time between movement initiation and termination (when the cursor reached the 6 cm target). Search time was defined as the time between movement termination and returning the cursor to the start position.

The hand angle data were baseline subtracted. The baseline was defined as the mean hand angle over all trials in the baseline block. Outlier trials were defined as trials in which the hand angle deviated by more than three standard deviations from a moving five-trial window, or in which the hand angle on a single trial was greater than 90° from the target, or in which participants moved unusually long (movement time greater than 1,000 ms). These trials were discarded since behaviour on these trials probably reflects attentional lapses and potential online corrections (average percentage of trials removed, 1.6 ± 2.1%).

The degree of adaptation was quantified as the change in hand angle in the opposite direction of the rotation. We calculated hand angle during early adaptation, late adaption and the aftereffect phase. Early adaptation was defined as the mean hand angle over the first ten trials during the rotation block. Late adaptation was defined as the mean hand angle over the last ten trials during the rotation block. Aftereffect was operationalized as the mean hand angle during the no-feedback block.

The hand angle data during the early, late and aftereffect phases were entered into a circular Gaussian mixture model to identify potential subgroups (R package BAMBI<sup>134</sup> v.2.3.5). The best model was determined on the basis of BIC. The hand angle data were then entered into a group lasso regression as dependent variables (R function cv.glmnet<sup>135</sup>), and all the features in Table 1 were entered as independent predictors. Categorical variables were assigned dummy variables<sup>136</sup>; continuous variables were z-scored<sup>137</sup>. We conducted a group lasso regression because it penalizes unimportant independent variables (that is, sets them to zero) and therefore is very conservative in terms of identifying predictors. Group lasso also forces the model to keep or discard pre-defined sets of grouped variables (for example, undergraduate major).

A priori, we used tenfold cross-validation on 80% of the sessions to select the model with the minimum mean cross-validation error. We fixed the best-performing model's  $\beta$  values and evaluated the degree to which this model predicted held-out data (the remaining 20% of sessions). We used the coefficient of determination ( $R_{cv}^2$ ) between the predicted and the actual held-out data as our key metric of model performance. Post hoc, we evaluated  $R_{cv}^2$  across combinations of folds (4–15 folds) and percentages of held-out data (50–90%). This sensitivity analysis allowed us to evaluate how our results compare to those obtained with different hyperparameter settings. In addition, we obtained  $\beta$  CIs by entering bootstrap-resampled data 1,000 times with replacement (using the same training data) into the group lasso regression. Note that cross-validated lasso regression is fairly robust to multi-collinearity<sup>106</sup>.

### Model-based simulations

We simulated the data for the competition theory<sup>84</sup> and the independence theory<sup>138</sup> (see the open-sourced code for more details on the various parameter settings). Both theories posit that overall performance ( $y_n$ ) reflects the joint contribution of implicit ( $x_n^i$ ) and explicit processes ( $x_n^e$ ):

$$y_n = N(x_n^i + x_n^e, \sigma_M) \quad (1)$$

where  $n$  is trial number and  $\sigma_M$  is motor noise (equation (1)). However, the two theories diverge in terms of the learning signal that drives each process. The competition theory postulates that task error ( $e_n^t$ ; equation (2), where  $r$  is the rotation size)—the difference between the cursor and the goal—drives both implicit and explicit processes (equations (3) and (4), where  $A^i$  is the implicit retention rate,  $B^i$  is the implicit learning rate,  $A^e$  is the explicit retention rate and  $B^e$  is the explicit learning rate):

$$e_n^t = r - y_n \quad (2)$$

$$x_{n+1}^i = A^i x_n^i + B^i e_n^t \quad (3)$$

$$x_{n+1}^e = A^e x_n^e + B^e e_n^t \quad (4)$$

The independence theory posits that task error drives explicit re-aiming (equation (2)), and sensory prediction error ( $e_n^s$ ; equation (5))—the mismatch between the predicted position (the aiming position) and the actual cursor position—drives implicit recalibration (equation (7)):

$$e_n^s = r - x_n^i \quad (5)$$

$$x_{n+1}^e = A^e x_n^e + B^e e_n^s \quad (6)$$

$$x_{n+1}^i = A^i x_n^i + B^i e_n^t \quad (7)$$

Furthermore, the independence theory often includes plan-based generalization, the phenomenon where the peak of implicit recalibration centres on the predicted (aiming) cursor position ( $x_n^e$ )<sup>139</sup>. As such, the aftereffect measured at the target ( $x_n^{i,m}$ ) is determined by equation (8), where  $\sigma_G$  is the width of generalization:

$$x_n^{i,m} = x_n^i e^{-\frac{(x_n^e)^2}{2\sigma_G^2}} \quad (8)$$

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

The data are available at <https://osf.io/5n7jf/>.

### Code availability

The analysis code is available at <https://osf.io/5n7jf/>.

### References

- Krakauer, J., Hadjiosif, A. M., Xu, J., Wong, A. L. & Haith, A. M. Motor learning. *Compr. Physiol.* **9**, 613–663 (2019).
- Roemmich, R. T. & Bastian, A. J. Closing the loop: from motor neuroscience to neurorehabilitation. *Annu. Rev. Neurosci.* **41**, 415–429 (2018).
- Tsay, J. S. & Winstein, C. J. Five features to look for in early-phase clinical intervention studies. *Neurorehabil. Neural Repair* **35**, 3–9 (2021).
- Helmholtz, H. L. F. V. *Treatise on Physiological Optics* (Dover, 1924).
- Stratton, G. M. Some preliminary experiments on vision without inversion of the retinal image. *Psychol. Rev.* **3**, 611–617 (1896).
- Ghilardi, M. et al. Patterns of regional brain activation associated with different forms of motor learning. *Brain Res.* **871**, 127–145 (2000).
- Krakauer, J., Pine, Z. M., Ghilardi, M. F. & Ghez, C. Learning of visuomotor transformations for vectorial planning of reaching trajectories. *J. Neurosci.* **20**, 8916–8924 (2000).
- Krakauer, J., Ghez, C. & Ghilardi, M. F. Adaptation to visuomotor transformations: consolidation, interference, and forgetting. *J. Neurosci.* **25**, 473–478 (2005).
- Ferreira, E., Franke, J., Morel, P. et al. Statistical determinants of visuomotor adaptation along different dimensions during naturalistic 3D reaches. *Sci. Rep.* **12**, 10198 (2022).
- Kagerer, F. A., Contreras-Vidal, J. L. & Stelmach, G. E. Adaptation to gradual as compared with sudden visuo-motor distortions. *Exp. Brain Res.* **115**, 557–561 (1997).
- Shadmehr, R., Smith, M. A. & Krakauer, J. Error correction, sensory prediction, and adaptation in motor control. *Annu. Rev. Neurosci.* **33**, 89–108 (2010).
- Kim, H. E., Avraham, G. & Ivry, R. B. The psychology of reaching: action selection, movement implementation, and sensorimotor learning. *Annu. Rev. Psychol.* <https://doi.org/10.1146/annurev-psych-010419-051053> (2020).
- McDougle, S. D., Ivry, R. B. & Taylor, J. A. Taking aim at the cognitive side of learning in sensorimotor adaptation tasks. *Trends Cogn. Sci.* **20**, 535–544 (2016).
- Hegele, M. & Heuer, H. Implicit and explicit components of dual adaptation to visuomotor rotations. *Conscious. Cogn.* **19**, 906–917 (2010).
- Benson, B. L., Anguera, J. A. & Seidler, R. D. A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *J. Neurophysiol.* **105**, 2843–2851 (2011).
- Redding, G. M. & Wallace, B. Adaptive spatial alignment and strategic perceptual-motor control. *J. Exp. Psychol. Hum. Percept. Perform.* **22**, 379–394 (1996).

17. Tsay, J. S. et al. Strategic processes in sensorimotor learning: reasoning, refinement, and retrieval. Preprint at *PsyArXiv* <https://doi.org/10.31234/osf.io/x4652> (2023).
18. Tsay, J. S. et al. The effect of visual uncertainty on implicit motor adaptation. *J. Neurophysiol.* <https://doi.org/10.1152/jn.00493.2020> (2021).
19. Kim, H. E., Morehead, R., Parvin, D. E., Moazzezi, R. & Ivry, R. B. Invariant errors reveal limitations in motor correction rather than constraints on error sensitivity. *Commun. Biol.* **1**, 19 (2018).
20. Herzfeld, D. J., Vaswani, P. A., Marko, M. K. & Shadmehr, R. A memory of errors in sensorimotor learning. *Science* **345**, 1349–1353 (2014).
21. Albert, S. T. et al. An implicit memory of errors limits human sensorimotor adaptation. *Nat. Hum. Behav.* <https://doi.org/10.1038/s41562-020-01036-x> (2021).
22. Redding, G. M. & Wallace, B. Effects on prism adaptation of duration and timing of visual feedback during pointing. *J. Mot. Behav.* **22**, 209–224 (1990).
23. Held, R., Efstatiou, A. & Greene, M. Adaptation to displaced and delayed visual feedback from the hand. *J. Exp. Psychol.* **72**, 887–891 (1966).
24. Kitazawa, S., Kohno, T. & Uka, T. Effects of delayed visual information on the rate and amount of prism adaptation in the human. *J. Neurosci.* **15**, 7644–7652 (1995).
25. Brudner, S. N., Kethidi, N., Graeupner, D., Ivry, R. B. & Taylor, J. A. Delayed feedback during sensorimotor learning selectively disrupts adaptation but not strategy use. *J. Neurophysiol.* **115**, 1499–1511 (2016).
26. Tsay, J. S., Irving, C. & Ivry, R. B. Signatures of contextual interference in implicit sensorimotor adaptation. *Proc. Biol. Sci.* **290**, 20222491 (2023).
27. Tsay, J. S., Kim, H., Haith, A. M., & Ivry, R. B. Understanding implicit sensorimotor adaptation as a process of proprioceptive re-alignment. *eLife* <https://doi.org/10.7554/eLife.76639> (2022).
28. Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J. & Thach, W. T. Throwing while looking through prisms: I. Focal olivocerebellar lesions impair adaptation. *Brain* **119**, 1183–1198 (1996).
29. Tzvi, E., Loens, S. & Donchin, O. Mini-review: the role of the cerebellum in visuomotor adaptation. *Cerebellum* <https://doi.org/10.1007/s12311-021-01281-4> (2021).
30. Tsay, J. S., Najafi, T., Schuck, L., Wang, T. & Ivry, R. B. Implicit sensorimotor adaptation is preserved in Parkinson's disease. *Brain Commun.* **4**, fcac303 (2022).
31. Tsay, J. S., Schuck, L., & Ivry, R. B. Cerebellar degeneration impairs strategy discovery but not strategy recall. *Cerebellum* <https://doi.org/10.1007/s12311-022-01500-6> (2022).
32. Mutha, P. K., Sainburg, R. L. & Haaland, K. Y. Left parietal regions are critical for adaptive visuomotor control. *J. Neurosci.* **31**, 6972–6981 (2011).
33. Smith, M. A. & Shadmehr, R. Intact ability to learn internal models of arm dynamics in Huntington's disease but not cerebellar degeneration. *J. Neurophysiol.* **93**, 2809–2821 (2005).
34. Henrich, J., Heine, S. J. & Norenzayan, A. The weirdest people in the world? *Behav. Brain Sci.* **33**, 61–83 (2010). Discussion 83–135.
35. Yarkoni, T. & Westfall, J. Choosing prediction over explanation in psychology: lessons from machine learning. *Perspect. Psychol. Sci.* **12**, 1100–1122 (2017).
36. Wang, X., Abdullah, B. & Samsudin, S. The effect of contextual interference on motor learning among healthy adolescents: a systematic review. *J. Posit. Sch. Psychol.* **6**, 4545–4580 (2022).
37. Shewokis, P. A. Is the contextual interference effect generalizable to computer games? *Percept. Mot. Skills* **84**, 3–15 (1997).
38. Kantner, L. A., Segall, M. H., Campbell, D. T. & Herskovits, M. J. The influence of culture on visual perception. *Stud. Art. Educ.* **10**, 68–71 (1968).
39. Pitt, B., Carstensen, A., Boni, I., Piantadosi, S. T. & Gibson, E. Different reference frames on different axes: space and language in indigenous Amazonians. *Sci. Adv.* **8**, eabp9814 (2022).
40. Anderson, D. I., Lohse, K. R., Lopes, T. C. V. & Williams, A. M. Individual differences in motor skill learning: past, present and future. *Hum. Mov. Sci.* **78**, 102818 (2021).
41. Seidler, R. D. & Carson, R. G. Sensorimotor learning: neurocognitive mechanisms and individual differences. *J. Neuroeng. Rehabil.* <https://doi.org/10.1186/s12984-017-0279-1> (2017).
42. Ranganathan, R., Cone, S. & Fox, B. Predicting individual differences in motor learning: a critical review. *Neurosci. Biobehav. Rev.* **141**, 104852 (2022).
43. Ackerman, P. L. Determinants of individual differences during skill acquisition: cognitive abilities and information processing. *J. Exp. Psychol. Gen.* **117**, 288–318 (1988).
44. Fleishman, E. A. On the relation between abilities, learning, and human performance. *Am. Psychol.* **27**, 1017–1032 (1972).
45. Tsay, J. S., Lee, A., Ivry, R. B., & Avraham, G. Moving outside the lab: the viability of conducting sensorimotor learning studies online. *Neurons Behav. Data Anal.* <https://doi.org/10.51628/001c.26985> (2021).
46. Tsay, J. S. et al. OnPoint: a package for online experiments in motor control and motor learning. Preprint at *PsyArXiv* <https://doi.org/10.31234/osf.io/hwmpy> (2020).
47. Germine, L. et al. Is the Web as good as the lab? Comparable performance from Web and lab in cognitive/perceptual experiments. *Psychon. Bull. Rev.* **19**, 847–857 (2012).
48. Germine, L. T., Duchaine, B. & Nakayama, K. Where cognitive development and aging meet: face learning ability peaks after age 30. *Cognition* **118**, 201–210 (2011).
49. Wilmer, J. B. et al. Capturing specific abilities as a window into human individuality: the example of face recognition. *Cogn. Neuropsychol.* **29**, 360–392 (2012).
50. Kim, H. et al. Multiracial Reading the Mind in the Eyes Test (MRMET): an inclusive version of an influential measure. Preprint at OSF <https://doi.org/10.31219/osf.io/y8djm> (2022).
51. Wilmer, J. B. How to use individual differences to isolate functional organization, biology, and utility of visual functions; with illustrative proposals for stereopsis. *Spat. Vis.* **21**, 561–579 (2008).
52. Bond, K. & Taylor, J. A. Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *J. Neurophysiol.* **113**, 3836–3849 (2015).
53. Shyr, M. C. & Joshi, S. S. A case study of the validity of web-based visuomotor rotation experiments. *J. Cogn. Neurosci.* **36**, 71–94 (2024).
54. Kim, O. A., Forrence, A. D. & McDougle, S. D. Motor learning without movement. *Proc. Natl Acad. Sci. USA* **119**, e2204379119 (2022).
55. Taylor, J. A., Krakauer, J. W. & Ivry, R. B. Explicit and implicit contributions to learning in a sensorimotor adaptation task. *J. Neurosci.* **34**, 3023–3032 (2014).
56. Anwyl-Irvine, A., Dalmajer, E.S., Hodges, N. et al. Realistic precision and accuracy of online experiment platforms, web browsers, and devices. *Behav. Res.* **53**, 1407–1425 (2021).
57. Flanagan, J. C. A simplified procedure for determining the reliability of a test by split-halves. *J. Educ. Psychol.* **28**, 99–103 (1937).
58. Allen, M. J. *Introduction to Measurement Theory* (Waveland, 1979).
59. Avraham, G., Morehead, R., Kim, H. E. & Ivry, R. B. Reexposure to a sensorimotor perturbation produces opposite effects on explicit and implicit learning processes. *PLoS Biol.* **19**, e3001147 (2021).

60. Tsay, J. S., Kim, H. E., Parvin, D. E., Stover, A. R. & Ivry, R. B. Individual differences in proprioception predict the extent of implicit sensorimotor adaptation. *J. Neurophysiol.* <https://doi.org/10.1152/jn.00585.2020> (2021).
61. Huberdeau, D. M., Krakauer, J. W. & Haith, A. M. Practice induces a qualitative change in the memory representation for visuomotor learning. *J. Neurophysiol.* <https://doi.org/10.1152/jn.00830.2018> (2019).
62. Haith, A. M., Huberdeau, D. M. & Krakauer, J. W. The influence of movement preparation time on the expression of visuomotor learning and savings. *J. Neurosci.* **35**, 5109–5117 (2015).
63. Morehead, R., Qasim, S. E., Crossley, M. J. & Ivry, R. Savings upon re-aiming in visuomotor adaptation. *J. Neurosci.* **35**, 14386–14396 (2015).
64. Schmitz, G. Enhanced cognitive performance after multiple adaptations to visuomotor transformations. *PLoS ONE* **17**, e0274759 (2022).
65. Tsay, J. S., Irving, C. & Ivry, R. B. Signatures of contextual interference in implicit sensorimotor adaptation. *Proc. R. Soc. B* **290**, 20222491 (2023).
66. Shea, J. B. & Morgan, R. L. Contextual interference effects on the acquisition, retention, and transfer of a motor skill. *J. Exp. Psychol. Hum. Learn.* **5**, 179–187 (1979).
67. Hadjiosif, A. M. & Smith, M. A. A double dissociation between savings and long-term memory in motor learning. *PLoS Biol.* **21**, e3001799 (2023).
68. Hadjiosif, A. M., Morehead, J. R. & Smith, M. A. A double dissociation between savings and long-term memory in motor learning. *PLoS Biol.* **21**, e3001799 (2023).
69. Joiner, W. M. & Smith, M. A. Long-term retention explained by a model of short-term learning in the adaptive control of reaching. *J. Neurophysiol.* **100**, 2948–2955 (2008).
70. Miyamoto, Y. R., Wang, S. & Smith, M. A. Implicit adaptation compensates for erratic explicit strategy in human motor learning. *Nat. Neurosci.* **23**, 443–455 (2020).
71. Roller, C. A., Cohen, H. S., Kimball, K. T. & Bloomberg, J. J. Effects of normal aging on visuo-motor plasticity. *Neurobiol. Aging* **23**, 117–123 (2002).
72. Buch, E. R., Young, S. & Contreras-Vidal, J. L. Visuomotor adaptation in normal aging. *Learn. Mem.* **10**, 55–63 (2003).
73. Vachon, C. M., Modchalingam, S., 't Hart, B. M. & Henriques, D. Y. P. The effect of age on visuomotor learning processes. *PLoS ONE* **15**, e0239032 (2020).
74. Wolpe, N. et al. Age-related reduction in motor adaptation: brain structural correlates and the role of explicit memory. *Neurobiol. Aging* <https://doi.org/10.1016/j.neurobiolaging.2020.02.016> (2020).
75. Wang, T. S. L., Martinez, M., Festa, E. K., Heindel, W. C. & Song, J.-H. Age-related enhancement in visuomotor learning by a dual-task. *Sci. Rep.* **12**, 5679 (2022).
76. Cressman, E. K., Salomonczyk, D. & Henriques, D. Y. P. Visuomotor adaptation and proprioceptive recalibration in older adults. *Exp. Brain Res.* **205**, 533–544 (2010).
77. Vandevoorde, K. & Orban de Xivry, J.-J. Why is the explicit component of motor adaptation limited in elderly adults? *J. Neurophysiol.* **124**, 152–167 (2020).
78. Wong, A. L., Marvel, C. L., Taylor, J. A. & Krakauer, J. W. Can patients with cerebellar disease switch learning mechanisms to reduce their adaptation deficits? *Brain* <https://doi.org/10.1093/brain/awy334> (2019).
79. Seidler, R. D. Differential effects of age on sequence learning and sensorimotor adaptation. *Brain Res. Bull.* **70**, 337–346 (2006).
80. Ruitenberg, M. F. L., Koppelmans, V., Seidler, R. D. & Schomaker, J. Developmental and age differences in visuomotor adaptation across the lifespan. *Psychol. Res.* <https://doi.org/10.1007/s00426-022-01784-7> (2023).
81. Vandevoorde, K. & Orban de Xivry, J.-J. Internal model recalibration does not deteriorate with age while motor adaptation does. *Neurobiol. Aging* **80**, 138–153 (2019).
82. Morehead, R. & de Xivry, J.-J. O. A synthesis of the many errors and learning processes of visuomotor adaptation. Preprint at bioRxiv <https://doi.org/10.1101/2021.03.14.435278> (2021).
83. Verstynen, T. & Kording, K. P. Overfitting to 'predict' suicidal ideation. *Nat. Hum. Behav.* **7**, 680–681 (2023).
84. Albert, S. T. et al. Competition between parallel sensorimotor learning systems. *eLife* <https://doi.org/10.7554/eLife.65361> (2022).
85. Tottenham, L. S. & Saucier, D. M. Throwing accuracy during prism adaptation: male advantage for throwing accuracy is independent of prism adaptation rate. *Percept. Mot. Skills* **98**, 1449–1455 (2004).
86. Zar, J. H. *Biostatistical Analysis: International Edition* 5th edn (Pearson, 2007).
87. Gajda, K., Sülzenbrück, S. & Heuer, H. Financial incentives enhance adaptation to a sensorimotor transformation. *Exp. Brain Res.* **234**, 2859–2868 (2016).
88. Tsay, J. S., Tan, S., Chu, M., Ivry, R. B. & Cooper, E. A. Low vision impairs implicit sensorimotor adaptation in response to small errors, but not large errors. *J. Cogn. Neurosci.* [https://doi.org/10.1162/jocn\\_a\\_01969](https://doi.org/10.1162/jocn_a_01969) (2023).
89. Burge, J., Ernst, M. O. & Banks, M. S. The statistical determinants of adaptation rate in human reaching. *J. Vis.* **8**, 20 (2008).
90. Kording, K. P. & Wolpert, D. M. Bayesian integration in sensorimotor learning. *Nature* **427**, 244–247 (2004).
91. McDougle, S. D. & Taylor, J. A. Dissociable cognitive strategies for sensorimotor learning. *Nat. Commun.* **10**, 40 (2019).
92. Fernandez-Ruiz, J., Wong, W., Armstrong, I. T. & Flanagan, J. R. Relation between reaction time and reach errors during visuomotor adaptation. *Behav. Brain Res.* **219**, 8–14 (2011).
93. Morehead, J. R. & Ivry, R. *Intrinsic Biases Systematically Affect Visuomotor Adaptation Experiments* (Society for Neural Control of Movement, 2015); [http://ivrylab.berkeley.edu/uploads/4/1/1/5/41152143/morehead\\_ncm2015.pdf](http://ivrylab.berkeley.edu/uploads/4/1/1/5/41152143/morehead_ncm2015.pdf)
94. Vindras, P., Desmurget, M., Prablanc, C. & Viviani, P. Pointing errors reflect biases in the perception of the initial hand position. *J. Neurophysiol.* **79**, 3290–3294 (1998).
95. Wilson, E. T., Wong, J. & Gribble, P. L. Mapping proprioception across a 2D horizontal workspace. *PLoS ONE* **5**, e11851 (2010).
96. McNay, E. C. & Willingham, D. B. Deficit in learning of a motor skill requiring strategy, but not of perceptuomotor recalibration, with aging. *Learn. Mem.* **4**, 411–420 (1998).
97. Fernández-Ruiz, J., Hall, C., Vergara, P. & Díaz, R. Prism adaptation in normal aging: slower adaptation rate and larger aftereffect. *Brain Res. Cogn. Brain Res.* **9**, 223–226 (2000).
98. Dhawale, A. K., Smith, M. A. & Ölveczky, B. P. The role of variability in motor learning. *Annu. Rev. Neurosci.* **40**, 479–498 (2017).
99. He, K. et al. The statistical determinants of the speed of motor learning. *PLoS Comput. Biol.* **12**, e1005023 (2016).
100. Wu, H. G., Miyamoto, Y. R., Castro, L. N. G., Ölveczky, B. P. & Smith, M. A. Temporal structure of motor variability is dynamically regulated and predicts motor learning ability. *Nat. Neurosci.* **17**, 312–321 (2014).
101. Singh, P., Jana, S., Ghosal, A. & Murthy, A. Exploration of joint redundancy but not task space variability facilitates supervised motor learning. *Proc. Natl Acad. Sci. USA* **113**, 14414–14419 (2016).
102. Behrens, T. E. J., Woolrich, M. W., Walton, M. E. & Rushworth, M. F. S. Learning the value of information in an uncertain world. *Nat. Neurosci.* **10**, 1214–1221 (2007).
103. Tsay, J. S., Kim, H., Haith, A. M. & Ivry, R. B. Understanding implicit sensorimotor adaptation as a process of proprioceptive re-alignment. *eLife* <https://doi.org/10.7554/eLife.76639> (2022).

104. Bönstrup, M., Iturrate, I., Hebart, M. N., Censor, N. & Cohen, L. G. Mechanisms of offline motor learning at a microscale of seconds in large-scale crowdsourced data. *NPJ Sci. Learn.* **5**, 7 (2020).
105. Taylor, J. A. & Ivry, R. B. Flexible cognitive strategies during motor learning. *PLoS Comput. Biol.* **7**, e1001096 (2011).
106. Hebiri, M. & Lederer, J. How correlations influence lasso prediction. *IEEE Trans. Inf. Theory* **59**, 1846–1854 (2013).
107. Burgoyne, A. P., Harris, L. J. & Hambrick, D. Z. Predicting piano skill acquisition in beginners: the role of general intelligence, music aptitude, and mindset. *Intelligence* **76**, 101383 (2019).
108. McGregor, H. R. & Gribble, P. L. Functional connectivity between somatosensory and motor brain areas predicts individual differences in motor learning by observing. *J. Neurophysiol.* **118**, 1235–1243 (2017).
109. Roberts, R. E., Bain, P. G., Day, B. L. & Husain, M. Individual differences in expert motor coordination associated with white matter microstructure in the cerebellum. *Cereb. Cortex* **23**, 2282–2292 (2013).
110. Landi, S. M., Baguer, F. & Della-Maggiore, V. One week of motor adaptation induces structural changes in primary motor cortex that predict long-term memory one year later. *J. Neurosci.* **31**, 11808–11813 (2011).
111. Koppelmans, V., Bloomberg, J. J., Mulavara, A. P. & Seidler, R. D. Brain structural plasticity with spaceflight. *NPJ Microgravity* <https://doi.org/10.1038/s41526-016-0001-9> (2016).
112. Pearson-Fuhrhop, K. M., Minton, B., Acevedo, D., Shahbaba, B. & Cramer, S. C. Genetic variation in the human brain dopamine system influences motor learning and its modulation by L-DOPA. *PLoS ONE* **8**, e61197 (2013).
113. Listman, J. B., Tsay, J. S., Kim, H. E., Mackey, W. E. & Heeger, D. J. Long-term motor learning in the ‘wild’ with high volume video game data. *Front. Hum. Neurosci.* **15**, 777779 (2021).
114. Aung, M. et al. Predicting skill learning in a large, longitudinal MOBA dataset. In *IEEE Conference on Computational Intelligence and Games (CIG)* 1–7 (IEEE, 2018).
115. Brookes, J., Warburton, M., Alghadier, M., Mon-Williams, M. & Mushtaq, F. Studying human behavior with virtual reality: the Unity Experiment Framework. *Behav. Res Methods* **52**, 455–463 (2020).
116. Chen, X. et al. Age-dependent Pavlovian biases influence motor decision-making. *PLoS Comput. Biol.* **14**, e1006304 (2018).
117. Donovan, I., Saul, M. A., DeSimone, K., Listman, J. B., Mackey, W. E., & Heeger, D. J. Assessment of human expertise and movement kinematics in first-person shooter games. *Front. Hum. Neurosci.* <https://doi.org/10.3389/fnhum.2022.979293> (2022).
118. Stafford, T. & Dewar, M. Tracing the trajectory of skill learning with a very large sample of online game players. *Psychol. Sci.* **25**, 511–518 (2014).
119. Stafford, T. & Vaci, N. Maximizing the potential of digital games for understanding skill acquisition. *Curr. Dir. Psychol.* <https://doi.org/10.1177/09637214211057841> (2022).
120. Balestrucci, P., Wiebusch, D. & Ernst, M. O. ReActLab: a custom framework for sensorimotor experiments ‘in-the-wild’. *Front. Psychol.* <https://doi.org/10.3389/fpsyg.2022.906643> (2022).
121. Kaur, J. & Balasubramaniam, R. Sequence learning in an online serial reaction time task: the effect of task instructions. *J. Mot. Learn. Dev.* 1–17 (2022).
122. Brantley, J. A. & Kording, K. P. Bayesball: Bayesian integration in professional baseball batters. Preprint at *bioRxiv* <https://doi.org/10.1101/2022.10.12.511934> (2022).
123. Drazan, J. F., Phillips, W. T., Seethapathi, N., Hullfish, T. J. & Baxter, J. R. Moving outside the lab: markerless motion capture accurately quantifies sagittal plane kinematics during the vertical jump. *J. Biomech.* **125**, 110547 (2021).
124. Hausmann, S. B., Vargas, A. M., Mathis, A. & Mathis, M. W. Measuring and modeling the motor system with machine learning. Preprint at *arXiv* <https://doi.org/10.48550/arXiv.2103.11775> (2021).
125. Hooyman, A. & Schaefer, S. Y. Age and sex effects on Super G performance are consistent across internet devices. *Int. J. Serious Games* **10**, 25–36 (2023).
126. Yin, C. & Wei, K. Savings in sensorimotor adaptation without explicit strategy. *J. Neurophysiol.* <https://doi.org/10.1152/jn.00524.2019> (2020).
127. Coltman, S. K., Cashaback, J. G. A. & Gribble, P. L. Both fast and slow learning processes contribute to savings following sensorimotor adaptation. *J. Neurophysiol.* **121**, 1575–1583 (2019).
128. Morehead, R., Taylor, J. A., Parvin, D. E. & Ivry, R. B. Characteristics of implicit sensorimotor adaptation revealed by task-irrelevant clamped feedback. *J. Cogn. Neurosci.* **29**, 1061–1074 (2017).
129. Maresch, J., Werner, S. & Donchin, O. Methods matter: your measures of explicit and implicit processes in visuomotor adaptation affect your results. *Eur. J. Neurosci.* <https://doi.org/10.1111/ejn.14945> (2020).
130. Hooyman, A., Huettelman, M. J., De Both, M., Ryan, L. & Schaefer, S. Y. Establishing the validity and reliability of an online motor learning game: applications for Alzheimer’s disease research within MindCrowd. *Games Health J.* <https://doi.org/10.1089/g4h.2022.0042> (2023).
131. Allen, K. R., Smith, K. A. & Tenenbaum, J. B. Rapid trial-and-error learning with simulation supports flexible tool use and physical reasoning. *Proc. Natl Acad. Sci. USA* **117**, 29302–29310 (2020).
132. Tsay, J. S., Schuck, L. & Ivry, R. B. Cerebellar degeneration impairs strategy discovery but not strategy recall. *Cerebellum* <https://doi.org/10.1007/s12311-022-01500-6> (2022).
133. Saban, W. & Ivry, R. B. PONT: a Protocol for Online Neuropsychological Testing. *J. Cogn. Neurosci.* 1–13 (2021).
134. Chakraborty, S. & Wong, S. W. K. BAMBI: An R package for fitting bivariate angular mixture models. *J. Stat. Softw.* **99**, 1–69 (2021).
135. Friedman, J., Hastie, T. & Tibshirani, R. Regularization paths for generalized linear models via coordinate descent. *J. Stat. Softw.* **33**, 1–22 (2010).
136. Choi, Y., Park, R. & Seo, M. Lasso on Categorical Data (CiteSeerX, 2012); <https://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.278.5439>
137. Tibshirani, R. Regression shrinkage and selection via the lasso. *J. R. Stat. Soc. B* **58**, 267–288 (1996).
138. McDougle, S. D., Bond, K. & Taylor, J. A. Implications of plan-based generalization in sensorimotor adaptation. *J. Neurophysiol.* **118**, 383–393 (2017).
139. Day, K. A., Roemmich, R. T., Taylor, J. A. & Bastian, A. J. Visuomotor learning generalizes around the intended movement. *eNeuro* <https://doi.org/10.1523/ENEURO.0005-16.2016> (2016).

## Acknowledgements

This project was supported by two NIH grants (no. 1F31NS120448 awarded to J.S.T. and no. R35NS116883-01 awarded to R.B.I.). The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

## Author contributions

J.S.T.: conceptualization, resources, data curation, software, formal analysis, funding acquisition, validation, investigation, visualization, methodology, project administration, writing—original

draft, writing—review and editing. H.A.: software, formal analysis, validation, investigation, visualization, methodology, writing—review and editing. L.T.G.: data curation, visualization, writing—review and editing. J.W.: data curation, visualization, writing—review and editing. R.B.I.: data curation, writing—review and editing, funding acquisition, validation, investigation, visualization. K.N.: data curation, writing—review and editing, validation, investigation, visualization, project administration.

## Competing interests

R.B.I. is a co-founder with equity in Magnetic Tides, Inc., a biotechnology company created to develop a novel method of non-invasive brain stimulation. The other authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at  
<https://doi.org/10.1038/s41562-023-01798-0>.

**Supplementary information** The online version contains supplementary material available at  
<https://doi.org/10.1038/s41562-023-01798-0>.

**Correspondence and requests for materials** should be addressed to Jonathan S. Tsay or Hrach Asmerian.

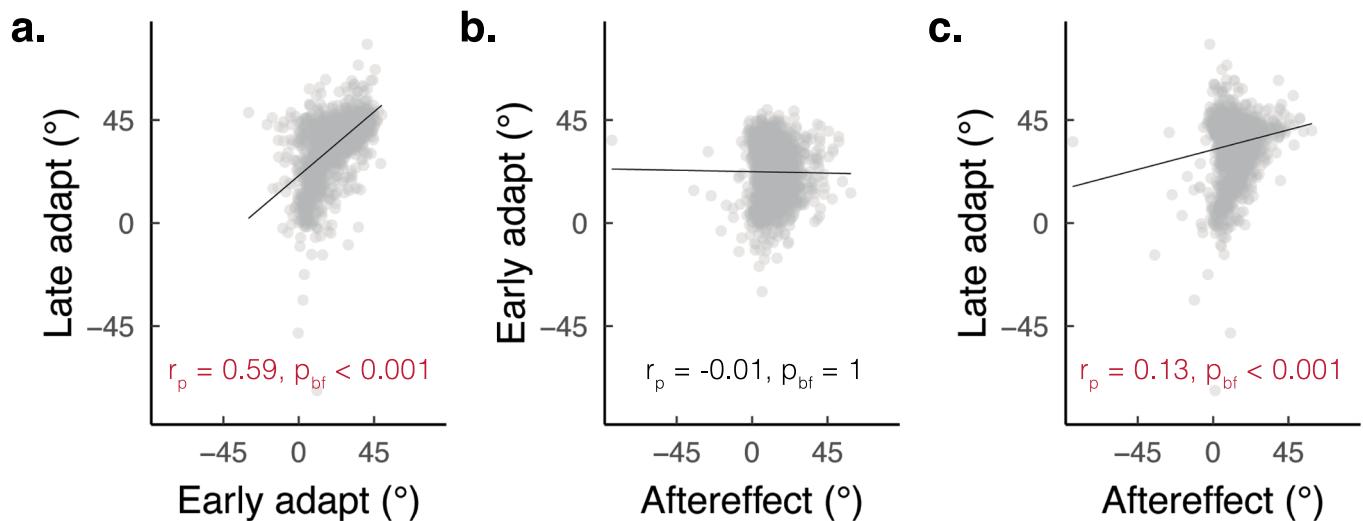
**Peer review information** *Nature Human Behaviour* thanks Joshua Cashaback, Scott T Albert, and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

**Reprints and permissions information** is available at [www.nature.com/reprints](http://www.nature.com/reprints).

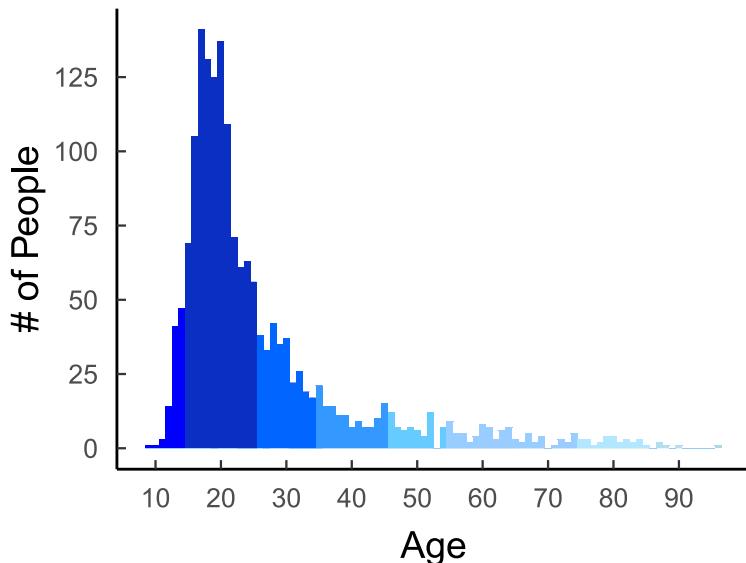
**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.

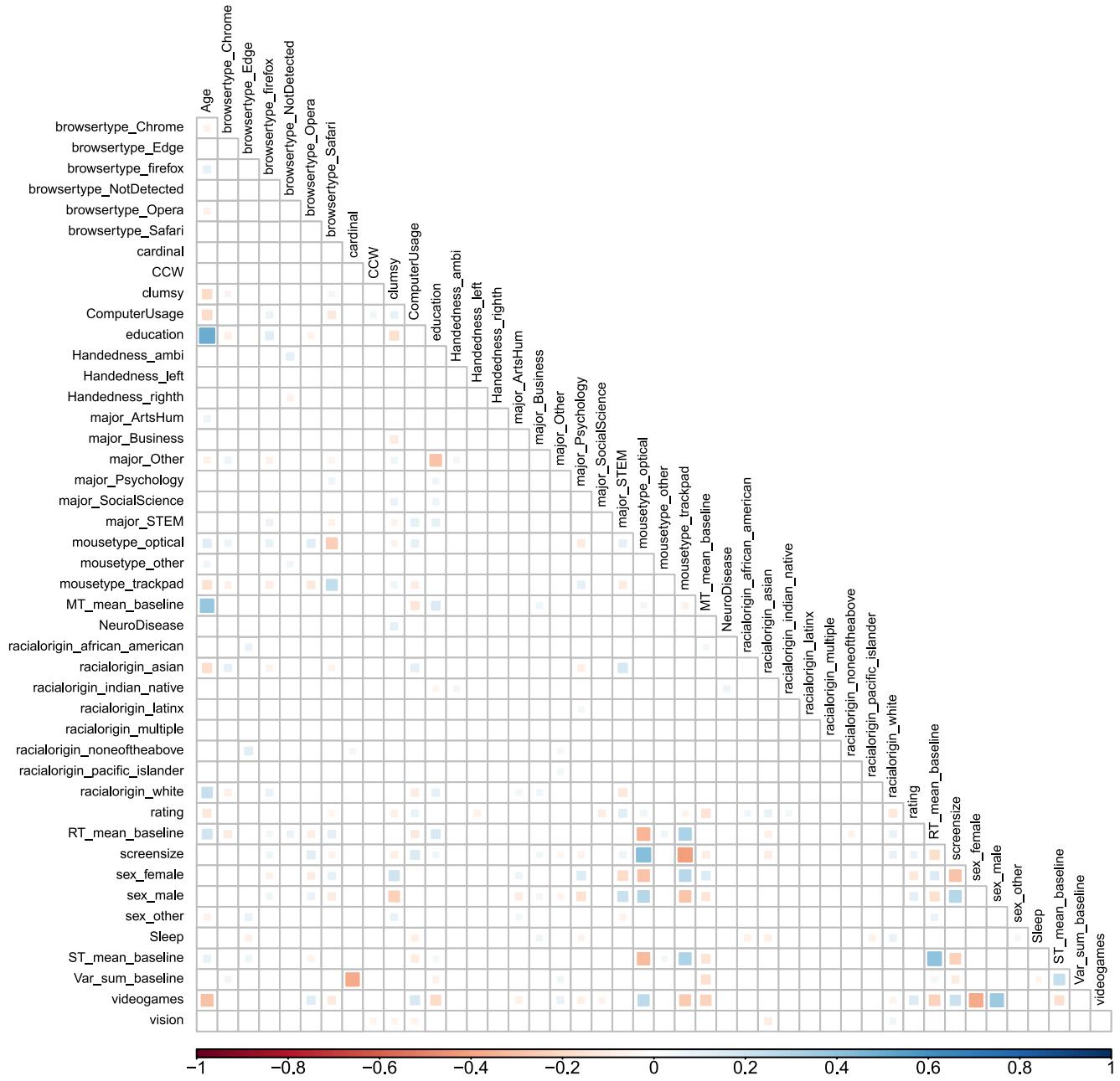
© The Author(s), under exclusive licence to Springer Nature Limited 2024



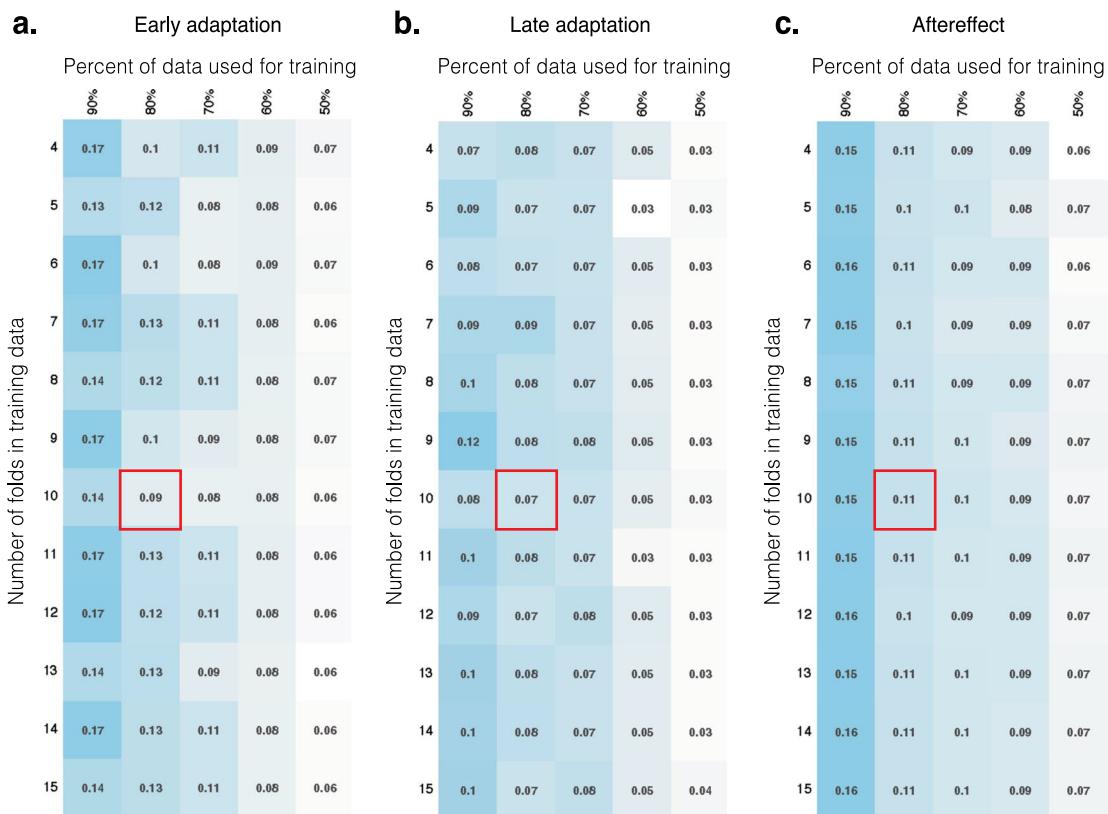
**Extended Data Fig. 1 | Correlations between different phases of motor adaptation.** Correlation between early and late adaptation (a), aftereffect and early adaptation (b), and aftereffect and late adaptation (c).  $r_p$  denotes Pearson's correlation (# of sessions = 1,747);  $p_{bf}$  denotes the p-value for a two-tailed t-test (Bonferroni-corrected for three comparisons).



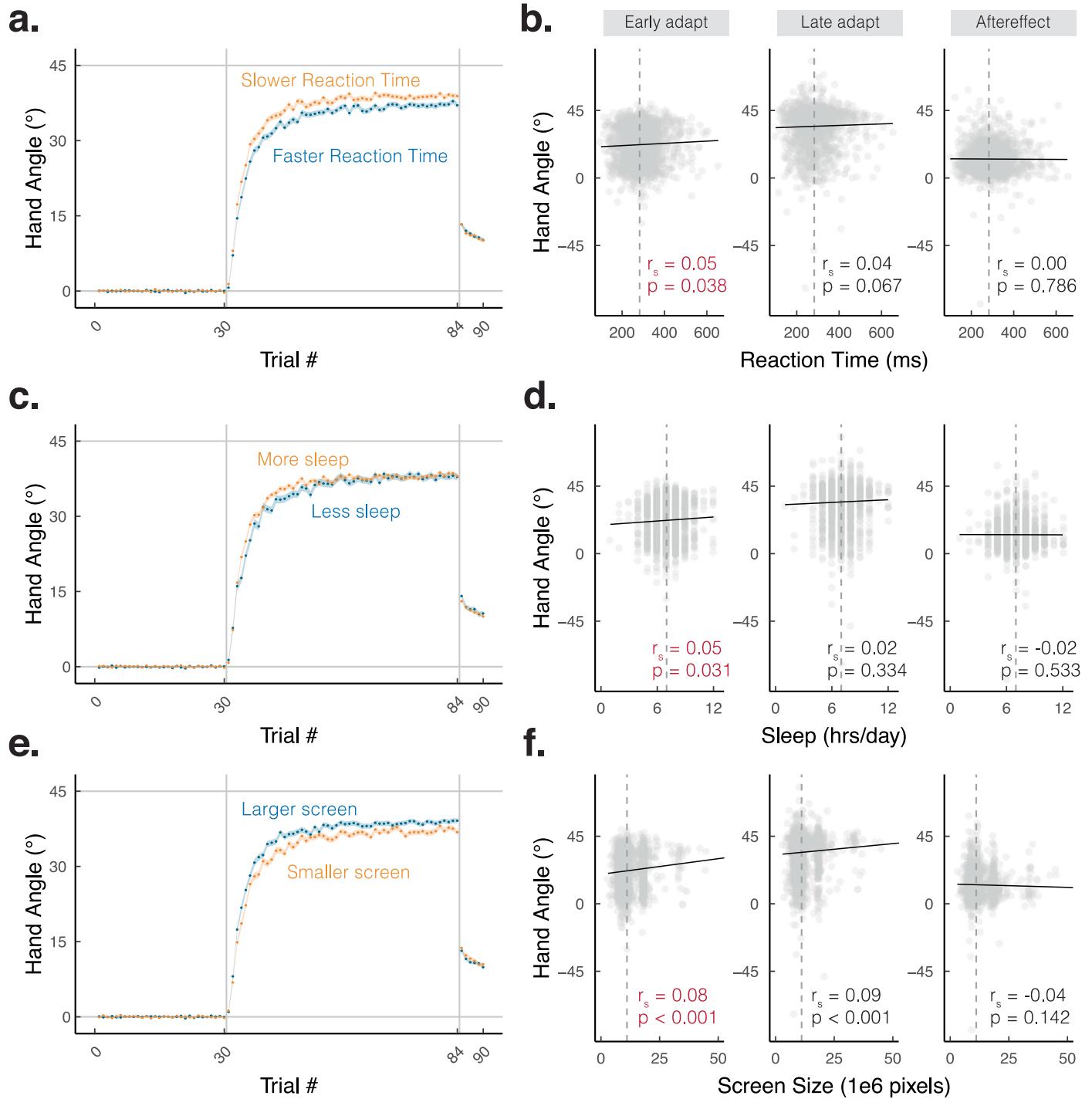
**Extended Data Fig. 2 | Age distribution.** Blue shading denotes different age groups (that is, rounded to the nearest decade). 107 individuals are closest to age 10, 1068 to age 20, 269 to age 30, 126 to age 40, 61 to age 50, 59 to age 60, 24 to age 70, 28 to age 80, and 5 to age 90. The oldest group was excluded in our aging analyses due to its limited sample size ( $n=5$ ).



**Extended Data Fig. 3 | Correlation matrix.** Color denotes the direction of the Pearson's correlations (# of sessions = 1,747), and square size denotes correlation magnitude.

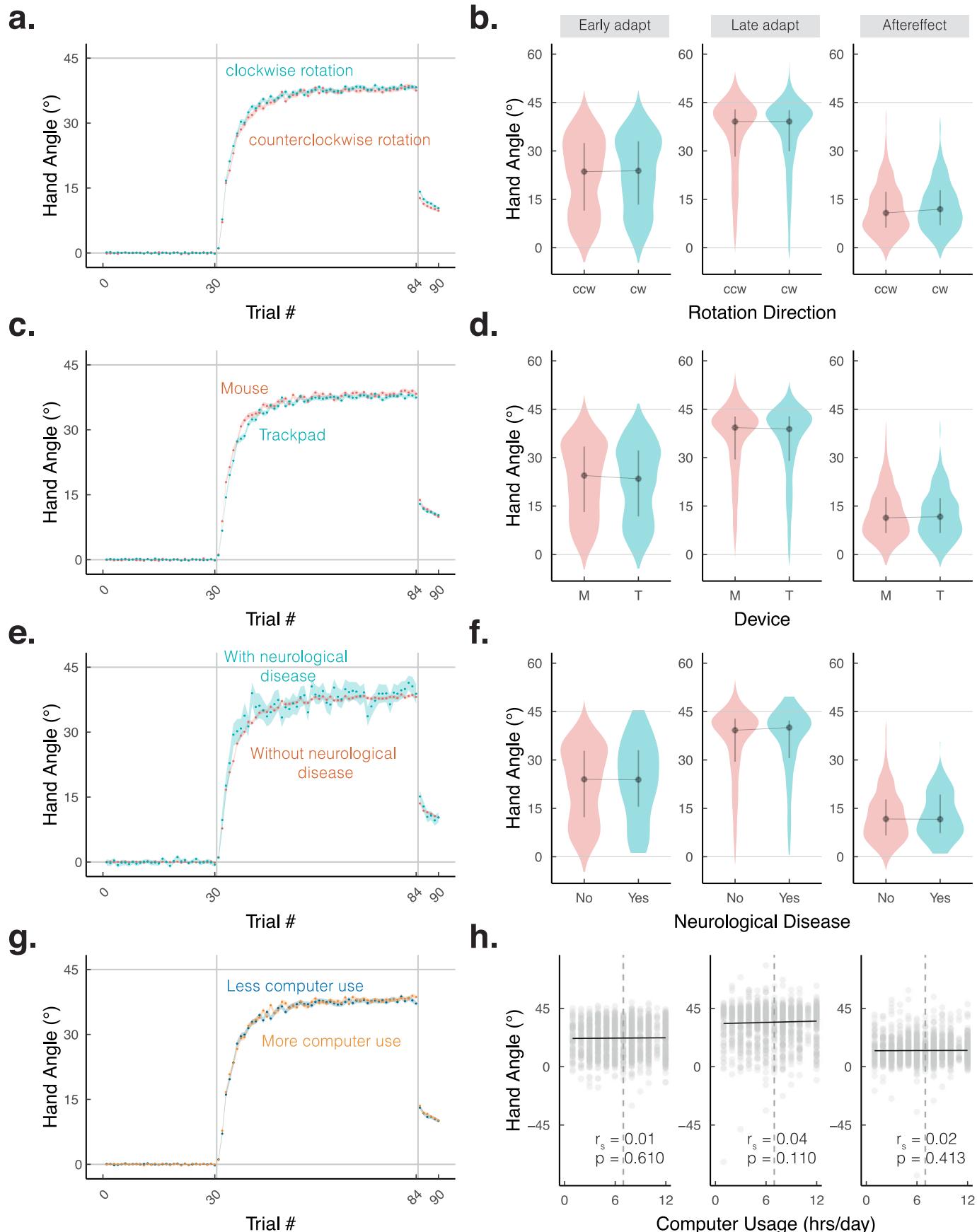


**Extended Data Fig. 4 | Results from our post-hoc Lasso regression were robust to changes in number of folds and percent of data used for training.** a–c, Shading and numbers denote the cross-validated coefficient of determination ( $R_{cv}^2$ ). The red box denotes the model used in this manuscript (that is, 80% training data split across 10-folds).



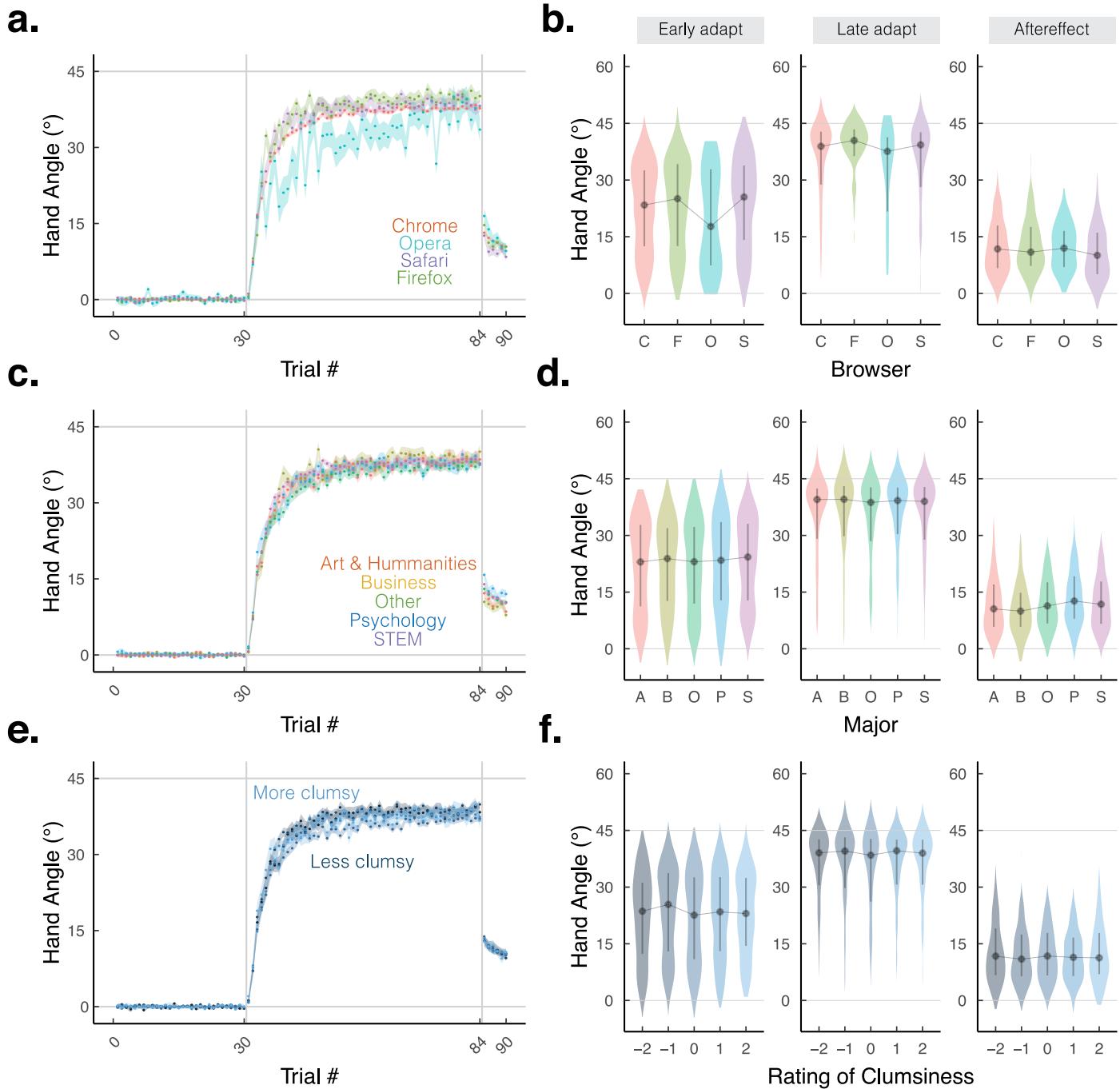
**Extended Data Fig. 5 | Features corresponding to Pattern 3 (continued).**  
**(a, b)** Baseline reaction time, **(c, d)** average amount of sleep every night, and **(e, f)** computer screen size. Left column: Data are presented as median values  $\pm$  SEM. Right column: The width of the violin plot represents data density. Vertical black

lines represent median values  $\pm$  1<sup>st</sup>/3<sup>rd</sup> IQR.  $r_s$  denotes Spearman's correlation; p value is obtained from a two-tailed t-test. We used data from 1,747 sessions (naïve participants who completed the one-target version of the task).



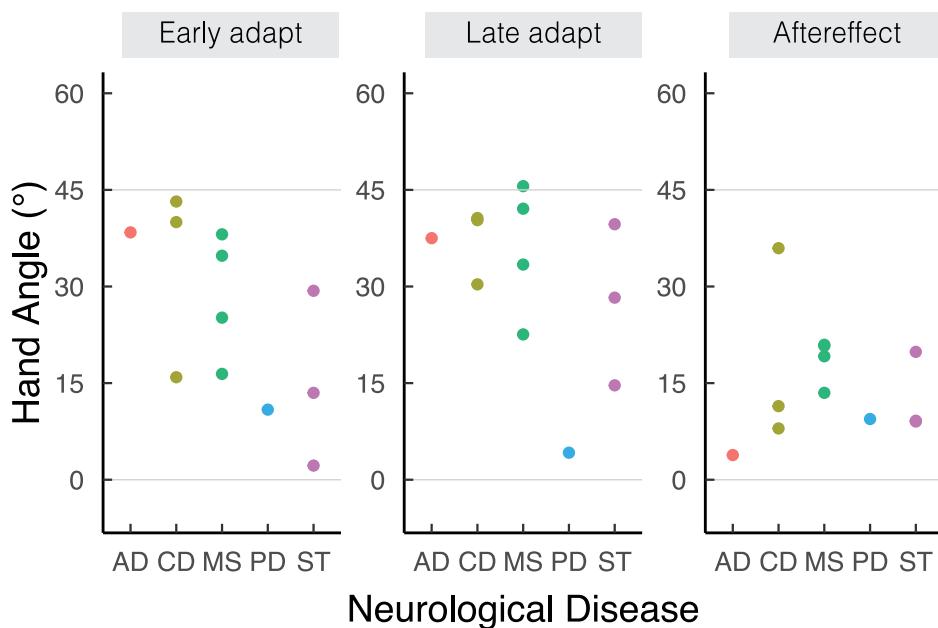
**Extended Data Fig. 6 | Features corresponding to Pattern 5.** (a, b) Perturbation direction, (c, d) device used, (e, f) self-reported neurological disease, and (g, h) amount of average computer usage. Left column: Data are presented as median values  $\pm$  SEM. Right column: The width of the violin plot represents data density.

Vertical black lines represent median values  $\pm 1^{\text{st}}/3^{\text{rd}}$  IQR.  $r_s$  denotes Spearman's correlation;  $p$  value is obtained from a two-tailed  $t$ -test. We used data from 1,747 sessions (naïve participants who completed the one-target version of the task).



**Extended Data Fig. 7 | Features corresponding to Pattern 5 (continued).**  
**(a, b)** Internet browser used, **(c, d)** undergraduate major, and **(e, f)** self-reported ratings of clumsiness. Left column: Data are presented as median values  $\pm$  SEM.

Right column: The width of the violin plot represents data density. Vertical black lines represent median values  $\pm$  1<sup>st</sup>/3<sup>rd</sup> IQR. We used data from 1,747 sessions (naïve participants who completed the one-target version of the task).



**Extended Data Fig. 8 | Self-reported neurological disease.** Among the 313 individuals reporting a neurological disease, only 12 described their specific disease, which we categorized into five main categories. AD: Alzheimer's Disease. CD: Cerebellar Degeneration. MS: Multiple Sclerosis. PD: Parkinson's Disease. ST: Stroke.

## Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

### Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size ( $n$ ) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided  
*Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g.  $F$ ,  $t$ ,  $r$ ) with confidence intervals, effect sizes, degrees of freedom and  $P$  value noted  
*Give P values as exact values whenever suitable.*
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's  $d$ , Pearson's  $r$ ), indicating how they were calculated

*Our web collection on [statistics for biologists](#) contains articles on many of the points above.*

### Software and code

Policy information about [availability of computer code](#)

Data collection All data were collected via a citizen science website, TestMyBrain.org.

Data analysis All analyses were conducted in R using only open-source libraries including BAMBI (version 2.3.5). All the analysis code is deposited in <https://osf.io/5n7jf/>

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

### Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

Data are available at: <https://osf.io/5n7jf/>. Analysis codes are available at: <https://osf.io/5n7jf/>.

## Human research participants

Policy information about [studies involving human research participants and Sex and Gender in Research](#).

Reporting on sex and gender	Our study involved participants from a diverse background, involving all sexes who performed the study on a citizen science website: testmybrain.org.
Population characteristics	Our study involved participants of all ages (ages: 9 - 96). All other population characteristics are summarized in Table 1.
Recruitment	Participants were recruited between 2019 and 2022 on a citizen science website (TestMyBrain.org) that provides personalized performance feedback in exchange for study participation. However, our results should be treated with caution for several reasons. First, the distribution of age groups were not balanced, with fewer participants at the extreme ends of the spectrum. Second, even though our study involved a highly heterogeneous sample, there may still exist some sample biases. For instance, our cohort may be more technologically proficient compared to the broader population, not to mention the limitation of participants primarily coming from English-speaking countries. To address these concerns, future studies are needed to not only recruit participants across age groups in a more balanced and uniform manner but also strive for a more diverse sample.
Ethics oversight	All participants provided their informed consent in accordance with policies approved by UC Berkeley's Institutional Review Board (Committee for Protection of Human Subjects: 2016-02-8439).

Note that full information on the approval of the study protocol must also be provided in the manuscript.

## Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences       Behavioural & social sciences       Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://nature.com/documents/nr-reporting-summary-flat.pdf)

## Behavioural & social sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	The data are quantitative and cross-sectional. Participants were recruited between 2019 and 2022 on a citizen science website (TestMyBrain.org) that provides personalized performance feedback in exchange for study participation. A total of 2,289 experimental sessions were collected. These data were used to examine the following questions 1) what is the effect of age on motor adaptation? 2) what is the effect of re-exposure to the same motor learning environment? 3) how are baseline kinematics distributed across the population? 4) what are the predictors of successful implicit and explicit motor adaptation?
Research sample	This study involves a diverse demography, consisting of computer users who conducted the experiment over a citizen science website. The relevant demographic information is provided in Table 1. We believe that the sample is relatively more representative than the college-age sample (given the relatively wide age range) and more heterogeneous than the typical WEIRD sample (given the level of diversity in racial origin and levels of education).
Sampling strategy	No a priori method was used to determine the sample size. The experiment was placed on the citizen science website for a predetermined two year period (time-frame sampling), and all the data were analyzed.
Data collection	All participants used their own laptop or desktop computer to access TestMyBrain.org that hosted the experiment (see a demo of the task at: <a href="https://multiclamp-c2.web.app/">https://multicclamp-c2.web.app/</a> ). Participants made reaching movements by moving the computer cursor with their mouse or trackpad. The participants were unaware of the experiment's objectives, and no blinding procedures were implemented for the experimenters.
Timing	Data were collected between January 2019 to December 2022.
Data exclusions	A total of 2,289 experimental sessions were collected. We excluded 168 sessions with erratic movements (i.e., the standard deviation of hand angle exceeded 25deg, or more than 20% of outlier datapoints were removed; see Data Analysis) or systematic movements to the wrong direction (i.e., mean heading angle less than 0deg or exceeded 75deg), leaving 2,121 eligible sessions.
Non-participation	No participants explicitly dropped-out or declined participation in our study.
Randomization	Participants were volunteered (self-selected) to participate for our study. Each individual was randomly assigned a single target location selected from a set of eight possible locations (cardinal targets: 0°, 90°, 180°, 270°; diagonal targets: 45°, 135°, 225°, 315°). Each individual was also randomly assigned a rotation/perturbation direction (45° clockwise or 45° counterclockwise).

# Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

## Materials & experimental systems

n/a	Involved in the study
<input checked="" type="checkbox"/>	Antibodies
<input checked="" type="checkbox"/>	Eukaryotic cell lines
<input checked="" type="checkbox"/>	Palaeontology and archaeology
<input checked="" type="checkbox"/>	Animals and other organisms
<input checked="" type="checkbox"/>	Clinical data
<input checked="" type="checkbox"/>	Dual use research of concern

## Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	ChIP-seq
<input checked="" type="checkbox"/>	Flow cytometry
<input checked="" type="checkbox"/>	MRI-based neuroimaging