Moving outside the lab: The viability of conducting sensorimotor learning studies online

Jonathan S. Tsay^{1,2}, Alan S. Lee¹, Richard B. Ivry^{1,2}, Guy Avraham^{1,2}

¹Department of Psychology, University of California, Berkeley

²Helen Wills Neuroscience Institute, University of California, Berkeley

Corresponding author Information:

9 Jonathan Sanching Tsay 10 Name: xiaotsay2015@berkeley.edu Email: 11 2121 Berkeley Way, Berkeley, CA 94704 Address: 12

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Abstract

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17 Collecting data online via crowdsourcing platforms has proven to be a very efficient way to recruit individuals from a large 18 diverse sample. While many fields in psychology have embraced online studies, the field of motor learning has lagged 19 behind. We suspect this is because of an implicit assumption that the loss of experimental control with online data collection 20 will be problematic for kinematic data. As a first foray to bring motor learning online, we developed a web-based platform 21 to collect kinematic data, serving as a template for researchers to create their own online sensorimotor control and learning 22 experiments. As a proof-of-concept, we present three visuomotor rotation experiments conducted with this platform, asking 23 if fundamental motor learning phenomena discovered in the lab could be reproduced online. In all experiments, there was a 24 close correspondence between the results obtained online with those previously reported from research conducted in the 25 laboratory. As such, our web-based motor learning platform can serve as a powerful tool to exploit the benefits of 26 27 crowdsourcing approaches and extend research on motor learning beyond the confines of the traditional laboratory. 28

Introduction 29

The ability to produce a wide repertoire of movements, and to adjust those movements in response to changes in the body 31 and environment, is a core feature of human competence. This ability helps a tired ping-pong player compensate for her 32 fatigue, and facilitates a patient's motor recovery from neurological injury (John W. Krakauer, Hadjiosif, Xu, Wong, & 33 Haith, 2019; Roemmich & Bastian, 2018; Jonathan S. Tsay & Winstein, 2020). By improving our understanding of how 34 movements are learned, we can uncover general principles about how the motor system functions and develops, optimize 35 training techniques for sport and rehabilitation, and design better brain-machine interfaces. 36

- A paradigmatic approach for studying motor learning is to introduce a new mapping between the motion of the arm and the 38 corresponding visual feedback (J. W. Krakauer, Pine, Ghilardi, & Ghez, 2000). Historically, such visuomotor perturbations 39 were accomplished by the use of prism glasses that distort the visual field (Helmholtz, 1924). Nowadays, virtual reality 40 setups allow more flexible control of the relationship between hand position and a feedback signal. A commonly used 41 perturbation is visuomotor rotation. Here, participants reach to a visual target with vision of the arm occluded. Feedback is 42 provided in the form of a cursor presented on a computer monitor. After a brief training period during which the feedback 43 corresponds to the actual hand position, a perturbation is introduced by rotating the position of the cursor from the actual 44 hand position (e.g., 15°). The mismatch between the expected and actual position of the feedback induces a change in the 45 heading direction of the hand, with the hand moving in the opposite direction of the rotation and thus reducing the mismatch 46 in subsequent trials. If the mismatch is small, this change will emerge in a gradual manner over trials and occurs outside the 47 participant's awareness, a phenomenon known as implicit sensorimotor adaptation. If the mismatch is large, this adaptive 48 learning process may also be accompanied by more explicit adjustments in aiming (Kim, Avraham, & Ivry, 2020; 49 McDougle, Ivry, & Taylor, 2016; Shadmehr, Smith, & Krakauer, 2010). 50
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Motor learning experiments are typically run in-person, exploiting finely calibrated apparatuses (digitizing tablets, robotic 52 manipulandum, full VR displays, etc.) that provide data with high temporal and spatial resolution. However, these 53 experiments come at a cost: Beyond the expenses associated with purchasing specialized equipment, the labor demands are 54 high for recruiting participants and administering the experiment, especially since testing is usually limited to one participant 55

at a time. In-person studies are also likely WEIRD (white, educated, industrialized, rich, and democratic), limiting the 56

generalizability of these research findings to the population writ large (Henrich, Heine, & Norenzayan, 2010). Moreover,
 exceptional circumstances that limit in-person testing, such as a global pandemic, may halt research progress (Fauci, Lane,
 & Redfield, 2020).

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Online experiments have been embraced across the social sciences as a powerful alternative approach for collecting data for behavioral experiments (Anwyl-Irvine, Massonnié, Flitton, Kirkham, & Evershed, 2020). Crowdsourcing platforms, such as Amazon Mechanical Turk (mturk.com) and Prolific (www.prolific.co), allow researchers to recruit a large number of participants, perform rapid pilot testing, and efficiently collect data using a variety of experimental designs. Compared to in-person studies, the online recruitment pool is likely to be more representative of the general population (Paolacci & Chandler, 2014). Online studies can also reach patient populations who have mobility deficits that limit their capability and willingness to come to the lab.

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Several studies have shown that the data obtained in online studies replicate those obtained from in-person studies (e.g., 69 Crump, McDonnell, & Gureckis, 2013). However, only a limited number of online studies have been performed in the 70 domain of sensorimotor learning. The field of motor learning may have shied away from these online methods because of 71 concerns related to the inherent loss of experimental control with online data collection, something that may be especially 72 problematic for kinematic data. Not only will the response devices be variable, but it would be difficult to control how 73 movements are produced between participants or even across the experimental session for a single participant. Previous 74 efforts examining motor learning in the wild (Chen et al., 2018; Crocetta et al., 2018; Fernandes, Albert, & Kording, 2011; 75 Haar, van Assel, & Faisal, 2020; John W. Krakauer et al., 2020; Takiyama & Shinya, 2016) have primarily focused on 76 testing specific hypotheses in their ecological setup, making it hard to directly compare their findings with those obtained 77 in the lab. Here we set out to create a general-purpose online platform that could be adopted by researchers for studying 78 sensorimotor control and learning. We report a series of experiments with designs commonly used to study sensorimotor 79 learning. We ask whether the data from our online studies replicate core phenomena reported in previous in-person studies. 80 The platform, OnPoint, is available on GitHub (Jonathan Sanching Tsay, Lee, et al., 2020), and participants were recruited 81 over Amazon's Mechanical Turk. The results show a close correspondence between the motor learning behavior observed 82 in-person and online, validating our tool as a platform for motor learning research, and serving as a proof-of-concept to 83 bring motor learning outside the confines of the traditional laboratory. 84

85 Results

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Experiment 1: Learning visuomotor rotation of different sizes

Motor learning is frequently treated as an implicit phenomenon. Indeed, expert performers frequently comment on letting 89 their "body do the thinking" when they execute an overlearned skill (Schmidt & Young, 1987). However, these experts are 90 also able to make rapid and flexible motor corrections, suggesting that even when behavior seems automatic, there remains 91 considerable cognitive control (Fitts & Posner, 1979). Recent work has highlighted how performance in even simple 92 sensorimotor adaptation tasks reflects the operation of multiple learning processes that may solve different computational 93 problems (Benson, Anguera, & Seidler, 2011; Diedrichsen, White, Newman, & Lally, 2010; Haith, Huberdeau, & Krakauer, 94 2015; Hegele & Heuer, 2010; Leow, Marinovic, de Rugy, & Carroll, 2018; Mazzoni & Krakauer, 2006; Miyamoto, Wang, 95 & Smith, 2020; Taylor, Krakauer, & Ivry, 2014; Werner et al., 2015). One source of evidence for this comes from a study 96 by Bond and Taylor (Bond & Taylor, 2015) who studied how people learn to respond when the visual feedback was rotated, 97 and in particular, when the size of the rotation was manipulated between 15° and 90° (Figure 1a). Explicit strategies, as 98 measured by verbal aim reports, were dominant when the error size was large, producing deviations in hand angle that 99 scaled with the size of the perturbation. Yet, implicit adaptation, as measured by aftereffects during a no-feedback block 100 that was introduced immediately after learning, remained constant over these perturbations. 101

Experiment 1 was designed to provide an online replication of Bond and Taylor (2015), testing whether the learning of visuomotor rotation – incorporating both explicit and implicit processes – scales with rotation size, and whether the aftereffect – reflecting solely the implicit process – remains constant across rotation sizes. After a series of baseline blocks to familiarize the participants with the apparatus and basic trial procedure, participants experienced one of four rotation sizes (15°, 30°, 60°, 90°), with the perturbation constant for an entire block of 80 rotation trials. Participants were instructed to make the cursor intersect the target; we did not specify if they should explicitly alter their aim to facilitate performance.

These learning functions are presented in Figure 1b (in-person, Bond and Taylor (2015)) and 1d (online version). We 110 analyzed our data together with those obtained by Bond and Taylor (2015), evaluating mean performance at three phases of 111 the experiment: Early adaptation, late adaptation, and aftereffect (Figures 1c and 1e). Learning scaled with the size of the 112 rotation during early learning (main effect of perturbation size: $F_{(1,136)} = 64.5$, p < 0.01), a signature of strategic aiming 113 at play. While there was no main effect of setting ($F_{(1,136)} = 0.5$, p = 0.46), adaptation scaled faster in the in-person group 114 compared to the online group (setting x perturbation size interaction: $F_{(1,136)} = 64.5$, p < 0.01). The mean angle during the 115 late phase of adaptation in all conditions reached an asymptote close to the size of the perturbation. As such, learning scaled 116 with the size of perturbation during the late phases of learning in both experiments ($F_{(1,136)} = 810.1, p < 0.01$). There was 117 neither a main effect of setting ($F_{(1,136)} = 1.3, p = 0.24$) nor an interaction between setting x perturbation size ($F_{(1,136)} = 1.3, p = 0.24$) 118 0.37, p = 0.54). 119

Hand angle dropped dramatically in the no-feedback aftereffect block, presumably due to the termination of aiming. However, the direction of the hand movements remained different than zero in the direction away from the feedback (all groups: p < 0.01), the signature of an implicit aftereffect. Critically, the magnitude of the aftereffect did not scale with the size of the rotation ($F_{(1,136)} = 2.5$, p = 0.12), indicating that implicit adaptation reaches a common saturation point, at least for the large range of values tested here. The magnitude of aftereffects was nominally similar to that reported in Bond and Taylor (2015) (main effect of setting: $F_{(1,136)} = 1.9$, p = 0.17), with the size of the aftereffect ranging from 0° to 30°. There was no interaction between setting x perturbation size in aftereffects ($F_{(1,136)} = 0.1$, p = 0.75).

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While the data from our online study are similar to the results from Bond and Taylor (2015), there were several notable 129 differences. First, within-participant variability was greater in the online group (In-person SD: $12.4 \pm 1.3^{\circ}$; Online SD: 130 $19.0 \pm 1.5^{\circ}$; p < 0.01). This may be due to the lack of stringent experimental supervision or differences in the types of 131 movements used in the in-person study (arm movements in Bond and Taylor) and online study (likely wrist and/or finger 132 movements given that most participants used a trackpad). Second, the online participants learned at a slower rate. This may 133 be because participants in the in-person study were able to identify and implement an aiming strategy faster than those tested 134 online. The lower variability for in-person movements is likely more conducive for identifying an appropriate strategy. 135 Alternatively, it may be easier to strategically adjust the aim of natural arm movements compared to the aim of finer 136 movements involving more distal joints over a trackpad. 137

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Third, and unexpectedly, the aftereffect data for the online participants was non-monotonic: More variance was explained 139 by a quadratic model ($R_{adj}^2 = 0.31, p < 0.01$) compared to a linear model ($R_{adj}^2 = 0.04, p = 0.29$), an effect that was not 140 present in the Bond and Taylor (2015) data, where neither a linear $(R_{adj}^2 = 0.06, p = 0.06)$ or quadratic function 141 $(Q: R_{adi}^2 = 0.05, p = 0.14)$ accounted for a significant percentage of variance. The reason for the non-monotonicity in the 142 online data is unclear. The dip for the 90° group might reflect some sort of discounting by the implicit system of this large, 143 non-ecological error (Berniker & Kording, 2008, 2011; Körding et al., 2007; Wei & Körding, 2009). However, the 144 aftereffect for this group was similar to that observed for the group exposed to a 15° rotation, the condition in which strategic 145 aiming is unlikely to make much, if any contribution (Morehead, Qasim, Crossley, & Ivry, 2015). An alternative possibility 146 is that the aftereffect data for the 30° and 60° groups are artifactually inflated by some residual effect of the aiming strategy 147 in the no-feedback aftereffect block. For example, there may have been a hysteresis effect when re-establishing the mapping 148 required to move straight to the target when using a trackpad or mouse, an effect that was not present for the 90°. It is also 149 possible that the extent of implicit adaptation as measured in the aftereffect data does vary with error size, albeit in a non-150 linear manner. We revisit this question using a different approach in Exp 2. 151 152

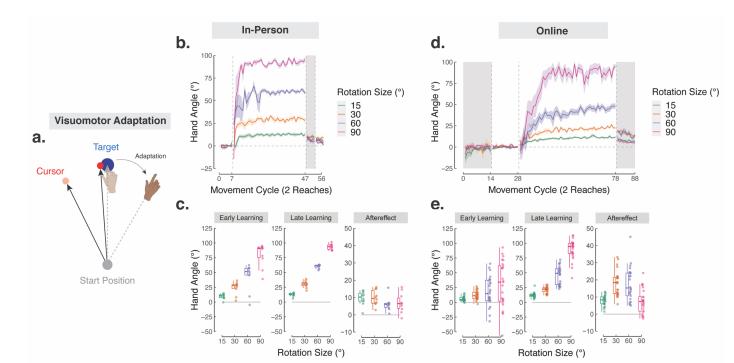


Figure 1. Sensorimotor learning in response to visuomotor rotations. (a) Schematic of a visuomotor rotation task. The cursor feedback (red dot) was rotated with respect to the movement direction of the hand, with the size of the rotation varied across groups $(15^\circ, 30^\circ, 60^\circ, or 90^\circ)$. Translucent and solid colors display hand and cursor positions at early and late stages of learning, respectively. (b, d) Mean time courses of hand angle for 15° (green), 30° (yellow), 60° (purple), and 90° (pink) rotation conditions from the in-person experiment of Bond and Taylor (2015) and the online experiment. Hand angle is presented relative to the target (0°) during veridical feedback, no-feedback (grey background), and rotation trials. Shaded region denotes SEM. (c, e) Average hand angles during early and late phases of the rotation block, and during the no-feedback aftereffect block from the in-person (c) and online (e) experiments. Box plots denote the median (thick horizontal lines), quartiles (1^{st} and 3^{rd} , the edges of the boxes), and extrema (min and max, vertical thin lines). The data from each participant is shown as translucent dots.

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Experiment 2: Adaptation in response to non-contingent rotated visual feedback

In Experiment 2, we turn to a method designed to measure implicit learning in the absence of strategic aiming. Motivated 157 by the idea that adaptation is obligatory in response to a visual sensory prediction error, Morehead et al. (Morehead, Taylor, 158 Parvin, & Ivry, 2017) replaced the standard movement-contingent visual feedback cursor with a "visual clamp". Here, the 159 cursor follows an invariant trajectory on all trials, with the radial position dependent on the participant's hand position (as 160 in standard feedback), but the angular position always shifted from the target by a fixed angle (Figure 2a). In this manner, 161 the angular position of the cursor is no longer contingent on the participant's movement. This manipulation, in combination 162 with instructions to ignore the cursor feedback and always move directly to the target, induces gradual changes in hand 163 angle away from the target in the direction opposite to the perturbation. Learning here is assumed to be entirely implicit, 164 verified in both subjective interviews provided by participants at the end of the experimental session (Kim, Morehead, 165 Parvin, Moazzezi, & Ivry, 2018; Kim, Parvin, & Ivry, 2019), as well as in reports of sensed hand location obtained on probe 166 trials throughout the adaptation block (Jonathan S. Tsay, Parvin, & Ivry, 2020). 167

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Given the assumption that learning is implicit, the clamp method provides another way to ask how error size influences implicit adaptation. Morehead et al (2017) demonstrated that the rate of adaptation is largely invariant over a wide range of error sizes (clamp angles ranging from $7.5^{\circ} - 95^{\circ}$). Moreover, the asymptote has also been shown to be independent of the error size for this range of perturbations, averaging between $15^{\circ} - 25^{\circ}$ across several studies (Avraham, Keizman, & Shmuelof, 2019; Kim et al., 2018; Jonathan S. Tsay, Avraham, et al., 2020; Jonathan S. Tsay, Kim, Parvin, Stover, & Ivry, 2020).

Experiment 2 used a design based on a subset of the conditions in Morehead et al (2017). We examined adaptation in response to visual clamps of 7.5°, 15°, and 30°, with each perturbation tested in separate groups of participants as in Experiment 1. We also included a 0° condition, one in which the cursor feedback always moved directly to the target. This condition provides a baseline to ensure that changes in hand angle in the other groups are driven by error-based learning, rather than changes due to fatigue or proprioceptive drift (Brown, Rosenbaum, & Sainburg, 2003a, 2003b; Cameron, de la Malla, & López-Moliner, 2015; Wann & Ibrahim, 1992).

These learning functions are presented in Figures 2b & 2d. We analyzed our data together with those obtained by Morehead et al (2017), evaluating mean performance at three phases of the experiment: Early adaptation, late adaptation, and aftereffect. As expected, there was no consistent change in performance in response to the 0° clamp in our data (one sample permutation test: early learning: p = 0.62; late adaptation, p = 0.87; aftereffects, p = 0.19), similar to that observed in Morehead et al (2017) (one sample permutation test: early learning, p = 0.46; late adaptation, p = 0.26; aftereffects, p =0.82). In contrast, adaptation was evident in all stages of learning for the non-zero clamps (one sample permutation test, all p < 0.05).

For non-zero clamp sizes, adaptation did not scale with rotation size during early learning ($F_{(1,86)} = 0.2, p = 0.66$), late learning ($F_{(1,86)} = 0.0, p = 0.91$), and the no-feedback aftereffect block ($F_{(1,86)} = 0.0, p = 0.96$) (Figures 2c and 2e). The 191 192 functions for the 7.5°, 15°, and 30° clamps reach a common asymptote around 15°, with the range of values across 193 individuals similar to that seen in the aftereffect data of Experiment 1. We note that the magnitude of adaptation is 194 approximately twice that of the perturbation for the 7.5° . While this might seem puzzling, it is important to keep in mind 195 that, unlike normal adaptation studies where the position of the feedback cursor is contingent on the hand movement and 196 thus, the size of the visual error is reduced throughout adaptation, the error size remains invariant with the clamped feedback 197 task and continues to drive adaptation. In terms of a comparison to in-person results, the online data were similar to those 198 collected by Morehead et al. (no main effect of setting: Early, $F_{(1,86)} = 0.8, p = 0.13$; Late, $F_{(1,86)} = 0.2, p = 0.63$, 199 Aftereffects, $F_{(1,86)} = 0.0, p = 0.98$). Within-participant variability was again greater in the online group (In-person SD: 200 $4.5 \pm 1.4^{\circ}$; Online SD: $8.2 \pm 0.4^{\circ}$; p < 0.01). 201

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In sum, these online results replicate two core insights that are derived from in-person studies using clamped feedback. 203 First, implicit adaptation occurs automatically in response to a visual sensory prediction error. Second, the learning function 204 is invariant across a large range of error sizes, both in the shape of the function and its asymptotic value. This invariance 205 poses a challenge to the standard state-space model of sensorimotor adaptation where the rate and magnitude of learning 206 are dependent on error size (Herzfeld, Vaswani, Marko, & Shadmehr, 2014; Marko, Haith, Harran, & Shadmehr, 2012; 207 Shadmehr et al., 2010; Smith, Ghazizadeh, & Shadmehr, 2006). Thus, the current results add additional evidence pointing 208 to the need for novel perspectives of adaptation, ones that do not assume adaptation to be sensitive to error size, but instead 209 constrained by the limits of sensorimotor plasticity (Kim et al., 2018) or sensory biases (Heald, Lengyel, & Wolpert, 2020; 210 Jonathan S. Tsay, Kim, et al., 2020). 211

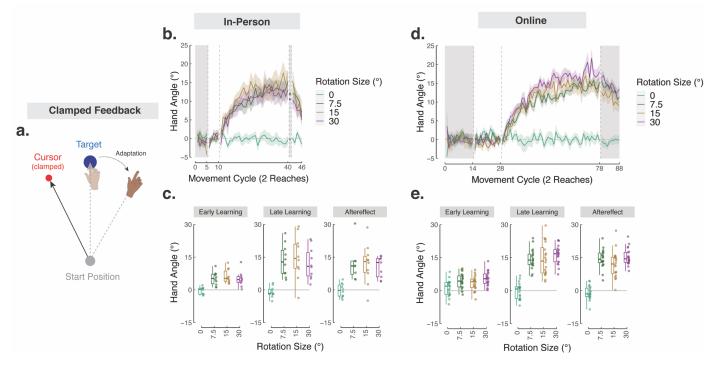


Figure 2. Sensorimotor adaptation in response to non-contingent displaced visual feedback. (a) Schematic of the clamped feedback task. The cursor feedback (red dot) follows a trajectory rotated relative to the target, independent of the position of the participant's hand. The rotation size remains invariant throughout the rotation block but varied across groups. Participants were instructed to move directly to the target (blue circle) and ignore the visual feedback. The translucent and solid colors display hand position early and late in learning, respectively. (b, d) Mean time courses of hand angle for 0° (green), 7.5° (dark green), 15° (brown), and 30° (dark purple) rotation conditions (in-person experiment, adapted from Morehead et al. 2017). Hand angle is presented relative to the target (0°) during no-feedback (dark grey background), veridical feedback, and rotation trials. Shaded region denotes SEM. (c, e) Average heading angles during early and late phases of the rotation block, and during the no-feedback aftereffect block from the in-person (c) and online (e) experiments. Box plots denote the median (thick horizontal lines), quartiles (1st and 3rd, the edges of the boxes), and extrema (min and max, vertical thin lines). The data from each participant is shown as translucent dots.

Experiment 3: Adaptation in response to variable, non-contingent rotated visual feedback

The use of a fixed perturbation for each participant in Experiments 1 and 2 allowed us to assess the full learning curve and 216 aftereffect. This design often lacks the power to identify subtle differences in sensitivity to error size because the standard 217 methods of analysis involve smoothing the data over multiple trials and making comparisons between individuals (or across 218 sessions if a repeated measures design is employed). An alternative approach to study the effect of error size on implicit 219 adaptation is to use a random perturbation schedule, exposing each individual to a range of error sizes throughout the 220 perturbation block. By including both clockwise and counterclockwise rotations, there is no cumulative measure of learning; 221 rather, the analysis focuses on trial-to-trial changes in heading angle (Figure 3a) (Avraham et al., 2019; Hutter & Taylor, 222 2018; Körding & Wolpert, 2004; Marko et al., 2012; Jonathan S. Tsay, Avraham, et al., 2020; Wei & Körding, 2009, 2010). 223 Even if the feedback is contingent on hand position, learning with this method is assumed to be entirely implicit since these 224 trial-by-trial perturbations, if relatively small, fall within the window of variation that arises from motor noise (Avraham et 225 al., 2019; Gaffin-Cahn, Hudson, & Landy, 2019). Variable perturbations can also be employed with non-contingent clamped 226 feedback, with the instructions providing a way to ensure that the behavioral changes are automatic and implicit. 227

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Following the in-person method used in Tsay et al (2020) (Jonathan Sanching Tsay, Haith, Ivry, & Kim, 2020), we varied the size of the non-contingent clamped feedback across trials. Each participant was exposed to a set of eight rotation sizes between 0 - 60°, with four of these involving clockwise rotations and the other four involving counterclockwise rotations of the same size. To sample a large range while keeping the experiment within 1 hour, participants received different sets of perturbations (total of four sets, see Methods). Given that the eight perturbations within a set have a mean of zero, there should be limited accumulated learning across trials. Similar to Experiment 2, participants were instructed to ignore the cursor feedback and always move directly to the target.

As a trial-by-trial measure of implicit adaptation, we averaged each participant's change in hand angle from trial n to trial n + 1, as a function of the rotation size on trial n. As can be seen in Figure 3c, the participants showed a sign-dependent change in hand angle in response to the clamped feedback, similar to that observed in the in-person study of Tsay et al. (Figure 3b, adapted from (Kasuga, Hirashima, & Nozaki, 2013; Kim et al., 2018; Ranjan & Smith, 2020; Jonathan S. Tsay,

Avraham, et al., 2020; Wei & Körding, 2009, 2010). The function is sublinear, composed of a quasi-linear zone for smaller perturbations (up to around 16°) and a saturation range for larger perturbations; indeed, the data suggest that the size of the trial-by-trial change in hand angle may fall off for the largest perturbations. In both the online and in-person studies, the mean changes in hand angle fall within a similar range ($\pm 2.5^{\circ}$).

To statistically evaluate these data, we first extracted the slope from each individual's learning function, asking whether this value was significantly less than 0. The slopes were significantly less than 0 for the online and in-person experiments (both p < 0.01), confirming robust sign-dependent implicit adaptation. We then asked whether the learning functions were sublinear by comparing, for each individual, the slope when computed using all perturbation sizes to the slope when using only the small perturbations (in-person: $0, \pm 4^{\circ}$; online: the smallest two rotation sizes in their set, maximum size = $\pm 25^{\circ}$). If the function is sublinear, the absolute slope calculated using all of the rotation sizes should be smaller (less negative). The results indicated that the functions were sublinear in both sets of data (in-person, p = 0.01; online, p = 0.02).

In sum, the results of Experiment 3 show a striking correspondence to that obtained in-person using a near-identical design (Kasuga, Hirashima, & Nozaki, 2013; Kim et al., 2018; Ranjan & Smith, 2020; Jonathan S. Tsay, Avraham, et al., 2020;
Wei & Körding, 2009, 2010). Moreover, the functions, both in shape and magnitude are quite similar to that reported in previous studies that have used a variable-sized perturbation to study implicit adaptation (Kasuga, Hirashima, & Nozaki, 2013; Kim et al., 2018; Ranjan & Smith, 2020; Jonathan S. Tsay, Avraham, et al., 2020; Wei & Körding, 2009, 2010).

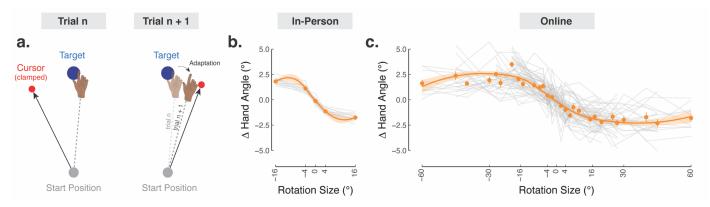


Figure 3. Trial-by-trial estimates of sensorimotor adaptation in response to variable, non-contingent visual feedback. (a) Schematic of the task. The cursor feedback (red dot) was rotated relative to the target, independent of the position of the participant's hand. The size of the rotation was varied randomly on a trial-by-trial basis. (b, c) The average change in hand angle from trial n to trial n + 1 is plotted as a function of rotation size on trial n. Thin grey lines are individual data collected in-person (b) and online (c), with the best-fitting loess line indicated by the orange curve (shaded region denotes SEM). Orange points denote group means and bars denote SEM.

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261 Discussion

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Bringing motor learning experiments online has considerable potential for providing researchers with a tool to collect data 263 from large and diverse samples in an efficient and low-cost method. As a proof-of-concept, we report here three experiments 264 examining behavioral changes in response to perturbed visual feedback, adopting established tasks for our online platform. 265 Qualitatively, the results from these three on-line studies show a close correspondence with those obtained from in-person 266 studies. Specifically, early and late learning scaled with the size of the rotation when both implicit and explicit processes 267 were involved (Exp 1), but implicit adaptation was insensitive to error size across a large range of errors (7.5° - 90° , Exps 268 1 and 2). In a more granular analysis, size sensitivity was found for smaller errors (Exp 3). These results, in aggregate. 269 demonstrate that online experiments provide a viable alternative to study sensorimotor adaptation outside the confines of 270 the traditional laboratory setting. 271

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These similarities between online and in-person experiments are especially striking in light of the many differences between 273 online and in-person settings. Almost all of the participants in our study reported using a trackpad (see Methods).[#] Although 274 we did not obtain detailed reports, we assume that their "reaching" movements here involved relatively small rotations about 275 the wrist, perhaps coupled with extension of the index finger. These types of movements will entail a very different set of 276 biomechanical and sensory constraints compared to reaches performed by moving along a digitizing tablet or when holding 277 a robotic manipulandum (de Rugy, Hinder, Woolley, & Carson, 2009; Debats & Heuer, 2018; Hollerbach & Flash, 1982; 278 Yin, Wang, Wei, & Körding, 2019). In-person experiments afford additional control, with the experimenter in a position to 279 provide verbal instructions, answer questions, and supervise the participant to ensure the movement is performed as desired. 280 This level of control is not possible with online studies where instructions are only given with on-screen messages and on-281 line monitoring is limited to feedback messages (e.g., "too far" or "too slow"). 282

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Another limitation with online experiments is greater uncertainty concerning the temporal delay of the feedback (Anwyl-284 Irvine, Dalmaijer, Hodges, & Evershed, 2020). This can be a critical factor for studies of adaptation given the evidence 285 showing that the rate of learning can fall off dramatically if the feedback is delayed, at least for endpoint feedback (Brudner, 286 Kethidi, Graeupner, Ivry, & Taylor, 2016; Held, Efstathiou, & Greene, 1966; Kitazawa, Kohno, & Uka, 1995). We have 287 observed this in our studies using clamped visual feedback. In our original study (Morehead, Taylor, Parvin, & Ivry, 2017), 288 the common asymptote across different error sizes was $\sim 15^{\circ}$. Subsequent to that study, we modified the code to reduce the 289 feedback delay (from around 70 ms to 25 ms). Using this refined code, Kim et al. (2018) also observed a common asymptote 290 in response to clamps of different sizes, but now the asymptotic values were $\sim 25^{\circ}$. For this reason, we would urge caution 291 in the use of online studies if the focus of the research is on absolute values such as the point of saturation. Concerns with 292 temporal delays are mitigated for relative comparisons (such as the analyses presented here to compare conditions in the 293 online studies). 294

In summary, online experiments provide a viable and novel way to test predictions about motor learning with large numbers 296 of participants in a short amount of time. Whereas it would have taken months to collect the data reported here if the studies 297 were run in-person, our online platform allowed us to collect these data in just a few days. Moreover, participants recruited 298 online represent greater diversity, one that spans a range in terms of age, ethnicity, handedness, and years of education (see 299 Participants) (Paolacci & Chandler, 2014). We do not envision online experiments replacing in-person testing in the domain 300 of sensorimotor control and learning, since the laboratory affords the means to capture kinematic data with unparalleled 301 precision. Nonetheless, many core phenomena central to our understanding of sensorimotor learning are robust and ripe for 302 online investigation. 303

[#] Because there were too few mouse users in each experiment, we opted not add device (trackpad or mouse) as a factor in our analysis. However, in an unpublished study using a standard visuomotor rotation, we tested 435 individuals, 205 who reported using a trackpad and 225 who reported using a mouse (5 opted to not provide this information or used some other response device). There were no differences in measures of adaptation for the two groups.

304 Methods

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306 Participants

The protocol was approved by the institutional review board at the University of California, Berkeley. Participants (n = 260; 308 age range = 21 - 61, mean age \pm sd = 34.6 ± 9.0) were recruited from the Amazon Mechanical Turk (AMT). Participants 309 received financial compensation for their participation at an \$8 per hour rate. Recruitment was restricted to the United 310 States. Based on the participants who completed an optional online survey (n = 180 out of 260 responded, 130 declined to 311 participate in the survey), there were 100 male participants, 69 female participants, and 11 identified as other. 124 of the 312 participants identified as White, 17 as Asian, 25 as African American, 1 as a Pacific-Islander, 2 as multi-racial, and 11 313 declined to answer. 144 of the participants were right-handed, 22 left-handed, and 4 self-identified as ambidextrous. In 314 terms of response devices, we encouraged participants to use a trackpad to limit variance from the device used. As a result, 315 there were 154 trackpad users but only 16 mouse users (others opted not to provide this information). No statistical methods 316 were used to determine the target sample sizes. 317

319 Apparatus

Participants used their own computer to access a dynamic webpage (HTML, JavaScript, and CSS) hosted on Google Firebase. The task progression was controlled by JavaScript code running locally in the participant's web browser. We assumed that monitor sampling rates were typically around 60 Hz, with little variation across computers (Anwyl-Irvine, Dalmaijer, et al., 2020). The size and position of stimuli were scaled based on each participant's screen size, which was automatically detected.

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A package containing all the codes of the experiment can be accessed and downloaded from GitHub (<u>https://github.com/alan-s-lee/OnPoint</u>) and Gorilla (<u>https://gorilla.sc/openmaterials/111001</u>). We also provided a user manual to assist other researchers in setting up motor learning experiments at <u>https://tinyurl.com/y6k8fvkk</u>.

331 Reaching Task Procedure

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The participant made reaching movements by moving the computer cursor with the trackpad or computer mouse. We did 333 not obtain information concerning the monitors used by each participant (something corrected in on-going studies); as such, 334 we cannot specify the size of the stimuli. However, from our experience in subsequent studies, we assume that most online 335 participants are using a laptop computer. To provide a rough sense of the stimulation conditions, we assume that the typical 336 monitor had a 13" screen with a width of 1366 pixels and height of 768 pixel (Anwyl-Irvine, Dalmaijer, et al., 2020). On 337 each trial, the participants made a center-out planar movement from the center of the workspace to a visual target. The 338 center position was indicated by a white circle (0.5 cm in diameter) and the target location was indicated by a blue circle 339 (also 0.5 cm in diameter). The radial distance of the target from the start location was 6 cm. In experiments 1 and 2, the 340 target could appear at one of two locations on an invisible virtual circle (45°: upper right quadrant; 135°: upper left quadrant). 341 For these experiments, a movement cycle is defined as 2 consecutive reaches, one to each target. In Experiment 3, the target 342 appeared in a single position at 45° throughout the entire experiment. 343

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To initiate each trial, the participant moved the cursor, represented by a white dot on their screen (0.5 cm in diameter), into 345 the start location. During this initialization phase, feedback was provided when the cursor was within 4 cm of the start circle. 346 Once the participant maintained the cursor in the start position for 500 ms, the target appeared. The location of the target in 347 Experiments 1 and 2 was selected in a pseudo-randomized manner. The participant was instructed to reach, attempting to 348 rapidly "slice" through the target. The feedback cursor, when presented (see below) remained visible throughout the duration 349 of the movement and remained fixed for 50 ms at the radial distance of the target when the movement amplitude reached 6 350 cm. If the movement was not completed within 500 ms, the message "too slow" was displayed in red 20 pt. Times New 351 Roman font at the center of the screen for 750 ms. 352

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The feedback could take one of the following forms: veridical feedback, no-feedback, rotated contingent feedback (Exp. 1), and rotated non-contingent ("clamped") feedback (Exps. 2 and 3). During veridical feedback trials, the movement direction of the visual feedback was veridical with respect to the movement direction of the hand. During no-feedback trials, the feedback cursor was extinguished as soon as the hand left the start circle and remained off for the entire reach. The cursor only became visible during the return phase of the trial, when the cursor was within 4 cm of the start circle. With rotated contingent feedback, the cursor moved at an angular offset relative to the position of the hand; the radial position of the

cursor corresponded to that of the hand up to 6 cm, at which point, the cursor position was frozen for 500 ms before turning off. During rotated clamped-feedback trials, the cursor moved at a specified angular offset relative to the position of the target, regardless of the movement direction of the hand ("clamped feedback"); as with rotated contingent feedback, the radial position of the cursor corresponded to that of the hand.

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Experiment 1: Learning visuomotor rotation of different sizes

AMT participants (N = 100) completed a visuomotor adaptation task consisting of four blocks of trials (178 trials total: 89 trials x 2 targets): Baseline no-feedback block (28 trials), baseline feedback block (28 trials), rotated feedback block (100 trials), and no-feedback aftereffect block (20 trials). During the rotation block, each participant was assigned one of four rotation sizes (15°, 30°, 60°, 90°; 25 participants/ group), with the direction of the rotation (clockwise or counterclockwise) counterbalanced across participants

Prior to each baseline block, the instruction "Move directly to the target as fast and accurately as you can" appeared on the screen. Prior to the rotation block, a new instruction message was presented: "Your cursor will now be rotated by a certain amount. In order to continue hitting the target, you will have to aim away from the target." Prior to the no-feedback aftereffect block, the participants were instructed "Move directly to the target as fast and accurately as you can."

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Experiment 2: Adaptation in response to non-contingent rotated visual feedback

A new sample of AMT participants (N = 80) completed a visuomotor adaptation task, with the same exact block structure as Experiment 1 (178 total trials). There was only one critical difference: Rotated, non-contingent feedback was used during the rotation block, with the clamp fixed at one of four angular offsets relative to the target (0°, 7.5°, 15°, 30°; 20 participants/group). The direction of the non-zero clamps (clockwise or counterclockwise) was counterbalanced across participants.

The instructions for baseline and no-feedback aftereffect blocks were identical to those used in Experiment 1. Prior to the rotation block, the instructions were modified to read: "The white cursor will no longer be under your control. Please ignore the white cursor and continue aiming directly towards the target." To clarify the invariant nature of the clamped feedback, three demonstration trials were provided. On all three trials, the target appeared straight ahead (90° position) and the participant was told to reach to the left (demo 1), to the right (demo 2), and backward (demo 3). On all three of these demonstration trials, the cursor moved in a straight line, 90° offset from the target. In this way, the participant could see that the spatial trajectory of the cursor was unrelated to their own reach direction.

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Experiment 3: Adaptation in response to variable, non-contingent rotated visual feedback

A new sample of AMT participants (N = 60) completed a visuomotor adaptation task consisting of four blocks of trials (255) 396 total trials): Baseline no-feedback block (5 trials), baseline feedback block (15 trials), rotated feedback block (230 trials), 397 and no-feedback aftereffect block (5 trials). During the rotation block, the non-contingent feedback varied from trial to trial, 398 both in direction (clockwise or counterclockwise) and angular offset. Participants were assigned one of four sets of rotation 399 sizes (Set 1: $\pm 2^{\circ}, \pm 4^{\circ}, \pm 6^{\circ}, \pm 20^{\circ}$; Set 2: $\pm 10^{\circ}, \pm 25^{\circ}, \pm 40^{\circ}, \pm 60^{\circ}$; Set 3: $\pm 7.5^{\circ}, \pm 15^{\circ}, \pm 30^{\circ}, \pm 45^{\circ}$; Set 4: $\pm 2^{\circ}, \pm 4^{\circ}, \pm 17^{\circ}$, 400 $+27^{\circ}$) where + indicates that the clamped feedback could be rotated clockwise (-) or counterclockwise (+). Given that eight 401 perturbations within a set have a mean of zero, the accumulated learning across trials should be limited. The same 402 demonstration trials (see Experiment 2) were included before the rotated clamped feedback block. 403

- 405 Attention and Instruction Checks
- 406

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It can be difficult to verify if participants tested online fully attend to the task. To mitigate this issue, we sporadically 407 instructed participants to make specific keypresses: "Press the letter "b" to proceed." If participants failed the make an 408 accurate keypress, the experiment was terminated. These attention checks were randomly introduced within the first 50 409 trials of the experiment. We also wanted to verify that the participants understand the task, and in particular, understood in 410 Experiments 2 and 3 that the angular position of the feedback was independent of the direction of their hand movement. To 411 this end, we included one instruction check after the three demonstration trials: "Identify the correct statement. Press 'a': I 412 will aim away from the target and ignore the white dot. Press 'b': I will aim directly towards the target location and ignore 413 the white dot." The experiment was terminated if participants failed to make an accurate keypress (i.e., "b"). 414

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416 Data Analysis

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The primary dependent variable of reach performance was hand angle, defined as the angle of the hand relative to the target when movement amplitude reached 6 cm from the start position (i.e., angle between a line connecting the start position to the target and a line connecting the start position to the hand). To aid visualization, the hand angle values for the groups (or trials in Experiment 3) with counterclockwise rotations were flipped, such that a positive hand angle corresponds to an angle in the opposite direction of the rotated feedback, the direction expected to result from learning.

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Outlier responses were defined as trials in which the hand angle deviated by more than 3 standard deviations from a moving 5-trial window. These outlier trials were excluded from further analysis since behavior on these trials could reflect attentional lapses or anticipatory movements to another target location (average percent of trials removed per participant: Experiment 1: $2.0 \pm 1.0\%$ Experiment 2: $1.5 \pm 1.1\%$ Experiment 3: $1.0 \pm 0.7\%$).

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Experiments 1 and 2: Data analysis mimicked the two studies we sought to replicate (Bond & Taylor, 2015; Morehead et 429 al., 2017). The mean heading angle for each movement cycle was calculated and baseline subtracted to evaluate adaptation 430 relative to idiosyncratic movement biases. Baseline was defined as the last 5 cycles of the verdical feedback baseline block 431 (cycles 24 - 28). We evaluated three hand angle measures: early adaptation, late adaptation, and aftereffect. Early adaptation 432 was operationalized as the average mean hand angle over cycles 31 - 35 (cycles 3-7 of the rotation block). Late adaptation 433 was defined as the mean hand angle over cycles 64 - 68 (cycles 35 - 40 of the rotation block, mimicking Bond and Taylor, 434 2015; and Kim et al, 2018). The aftereffect was operationalized as the average mean angle over the first 5 cycles of the no-435 feedback aftereffect block (cycles 79 - 83). 436

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All dependent measures were evaluated using an ANCOVA permutation test (R statistical packages: aovperm in the
 permuco package; 5000 permutations) as a more robust measure when the data is both normal and non-normally distributed
 (Lehmann and Romano 2008). Post-hoc pairwise permutation t-tests were performed (R statistical package: perm.t.test),
 and p values were Bonferroni correct to assess group differences.

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Experiment 3: As our measure of trial-by-trial adaptation, we calculated the change in hand angle on trial n + 1 as a function of the rotation size on trial n for each trial. Means were then calculated for each clamp size, averaging over the clockwise and counterclockwise perturbations for a given size. These mean data were submitted to a linear regression to extract each individual's slope (R statistical package: lm), with Rotation Size as the main effect. To ask whether these learning functions were sublinear, we compared each individual's slope computed with all four rotation sizes, against the slope computed with the two smallest rotation sizes in their set. If adaptation was sublinear, then the slopes computing using all rotation sizes would be smaller in absolute magnitudes (less negative) than the slope computed using only small rotation sizes.

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454 **References**

- Anwyl-Irvine, A. L., Dalmaijer, E. S., Hodges, N., & Evershed, J. (2020). Online Timing Accuracy and Precision: A
 comparison of platforms, browsers, and participant's devices. doi:10.31234/osf.io/jfeca
- Anwyl-Irvine, A. L., Massonnié, J., Flitton, A., Kirkham, N., & Evershed, J. K. (2020). Gorilla in our midst: An online
 behavioral experiment builder. *Behavior Research Methods*, 52(1), 388–407.
- Avraham, G., Keizman, M., & Shmuelof, L. (2020). Environmental Consistency Modulation of Error Sensitivity During
 Motor Adaptation is Explicitly Controlled. *Journal of Neurophysiology*. doi:10.1152/jn.00080.2019
- Benson, B. L., Anguera, J. A., & Seidler, R. D. (2011). A spatial explicit strategy reduces error but interferes with sensorimotor adaptation. *Journal of Neurophysiology*, *105*(6), 2843–2851.
- Berniker, M., & Kording, K. (2008). Estimating the sources of motor errors for adaptation and generalization. *Nature Neuroscience*, *11*(12), 1454–1461.
- Berniker, M., & Kording, K. P. (2011). Estimating the relevance of world disturbances to explain savings, interference and
 long-term motor adaptation effects. *PLoS Computational Biology*, 7(10), e1002210.
- Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology*, *113*(10), 3836–3849.
- Brown, L. E., Rosenbaum, D. A., & Sainburg, R. L. (2003a). Limb position drift: implications for control of posture and
 movement. *Journal of Neurophysiology*, *90*(5), 3105–3118.
- Brown, L. E., Rosenbaum, D. A., & Sainburg, R. L. (2003b). Movement speed effects on limb position drift. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *153*(2), 266–274.
- Brudner, S. N., Kethidi, N., Graeupner, D., Ivry, R. B., & Taylor, J. A. (2016). Delayed feedback during sensorimotor learning selectively disrupts adaptation but not strategy use. *Journal of Neurophysiology*, *115*(3), 1499–1511.
- Cameron, B. D., de la Malla, C., & López-Moliner, J. (2015). Why do movements drift in the dark? Passive versus active
 mechanisms of error accumulation. *Journal of Neurophysiology*, *114*(1), 390–399.
- Chen, X., Rutledge, R. B., Brown, H. R., Dolan, R. J., Bestmann, S., & Galea, J. M. (2018). Age-dependent Pavlovian
 biases influence motor decision-making. *PLoS Computational Biology*, *14*(7), e1006304.
- ⁴⁷⁹ Crocetta, T. B., de Araújo, L. V., Guarnieri, R., Massetti, T., Ferreira, F. H. I. B., de Abreu, L. C., & de Mello Monteiro, C.
- 480 B. (2018). Virtual reality software package for implementing motor learning and rehabilitation experiments. *Virtual*

Reality, 22(3), 199–209.

- 482 Crump, M. J. C., McDonnell, J. V., & Gureckis, T. M. (2013). Evaluating Amazon's Mechanical Turk as a tool for
- experimental behavioral research. *PloS One*, 8(3), e57410.
- de Rugy, A., Hinder, M. R., Woolley, D. G., & Carson, R. G. (2009). The synergistic organization of muscle recruitment
 constrains visuomotor adaptation. *Journal of Neurophysiology*, *101*(5), 2263–2269.
- Debats, N. B., & Heuer, H. (2018). Sensory integration of movements and their visual effects is not enhanced by spatial proximity. *Journal of Vision*, *18*(11), 15.
- Diedrichsen, J., White, O., Newman, D., & Lally, N. (2010). Use-dependent and error-based learning of motor behaviors.
 The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 30(15), 5159–5166.
- Fauci, A. S., Lane, H. C., & Redfield, R. R. (2020). [Review of *Covid-19 navigating the uncharted*]. *The New England journal of medicine*, 382(13), 1268–1269. Massachusetts Medical Society.
- Fernandes, H. L., Albert, M. V., & Kording, K. P. (2011). Measuring generalization of visuomotor perturbations in wrist
 movements using mobile phones. *PloS One*, 6(5), e20290.
- Fitts, P. M., & Posner, M. I. (1979). *Human performance*. Greenwood Press.
- Gaffin-Cahn, E., Hudson, T. E., & Landy, M. S. (2019). Did I do that? Detecting a perturbation to visual feedback in a
 reaching task. *Journal of Vision*, 19(1), 5.
- Haar, S., van Assel, C. M., & Faisal, A. A. (2020). Motor learning in real-world pool billiards. *Scientific Reports*, 10(1),
 20046.
- Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The influence of movement preparation time on the expression
- 500 of visuomotor learning and savings. *The Journal of Neuroscience: The Official Journal of the Society for* 501 *Neuroscience*, 35(13), 5109–5117.
- Heald, J. B., Lengyel, M., & Wolpert, D. M. (2020). Contextual inference underlies the learning of sensorimotor repertoires
 (p. 2020.11.23.394320). doi:10.1101/2020.11.23.394320
- Hegele, M., & Heuer, H. (2010). Implicit and explicit components of dual adaptation to visuomotor rotations. *Consciousness and Cognition*, 19(4), 906–917.
- Held, R., Efstathiou, A., & Greene, M. (1966). Adaptation to displaced and delayed visual feedback from the hand. *Journal of Experimental Psychology*, 72(6), 887–891.
- Helmholtz, H. L. F. V. (1924). Treatise on physiological optics. New York, NY: Dover Publications.

- 509 Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? The Behavioral and Brain Sciences,
- *33*(2–3), 61–83; discussion 83-135.
- Herzfeld, D. J., Vaswani, P. A., Marko, M. K., & Shadmehr, R. (2014). A memory of errors in sensorimotor learning.
 Science, 345(6202), 1349–1353.
- Hollerbach, M. J., & Flash, T. (1982). Dynamic interactions between limb segments during planar arm movement.
 Biological Cybernetics, 44(1), 67–77.
- Hutter, S. A., & Taylor, J. A. (2018). Relative sensitivity of explicit re-aiming and implicit motor adaptation (p. 308510).
 doi:10.1101/308510
- Kasuga, S., Hirashima, M., & Nozaki, D. (2013). Simultaneous processing of information on multiple errors in visuomotor
 learning. *PloS One*, 8(8), e72741.
- Kim, H. E., Avraham, G., & Ivry, R. B. (2020). The Psychology of Reaching: Action Selection, Movement Implementation,
 and Sensorimotor Learning. *Annual Review of Psychology*. doi:10.1146/annurev-psych-010419-051053
- Kim, H. E., Morehead, J. R., Parvin, D. E., Moazzezi, R., & Ivry, R. B. (2018). Invariant errors reveal limitations in motor
 correction rather than constraints on error sensitivity. *Communications Biology*, *1*, 19.
- Kim, H. E., Parvin, D. E., & Ivry, R. B. (2019). The influence of task outcome on implicit motor learning. *ELife*, 8.
 doi:10.7554/eLife.39882
- Kitazawa, S., Kohno, T., & Uka, T. (1995). Effects of delayed visual information on the rate and amount of prism adaptation
 in the human. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *15*(11), 7644–
 7652.
- Körding, K. P., Beierholm, U., Ma, W. J., Quartz, S., Tenenbaum, J. B., & Shams, L. (2007). Causal inference in
 multisensory perception. *PloS One*, 2(9), e943.
- 530 Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature*, 427(6971), 244–247.
- Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial
 planning of reaching trajectories. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 20(23), 8916–8924.
- Krakauer, John W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor Learning. *Comprehensive Physiology*, 9(2), 613–663.

- 536 Krakauer, John W., Kitago, T., Goldsmith, J., Ahmad, O., Roy, P., Stein, J., ... Luft, A. (2020). Comparing a novel
- neuroanimation experience to conventional therapy for high-dose, intensive upper-limb training in subacute stroke:
- 538 The SMARTS2 randomized trial. doi:10.1101/2020.08.04.20152538
- Leow, L.-A., Marinovic, W., de Rugy, A., & Carroll, T. J. (2018). Task errors contribute to implicit aftereffects in
 sensorimotor adaptation. *The European Journal of Neuroscience*, *48*(11), 3397–3409.
- Marko, M. K., Haith, A. M., Harran, M. D., & Shadmehr, R. (2012). Sensitivity to prediction error in reach adaptation.
 Journal of Neurophysiology, *108*(6), 1752–1763.
- Mazzoni, P., & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience, 26*(14), 3642–3645.
- McDougle, S. D., Ivry, R. B., & Taylor, J. A. (2016). Taking Aim at the Cognitive Side of Learning in Sensorimotor
 Adaptation Tasks. *Trends in Cognitive Sciences*, 20(7), 535–544.
- Miyamoto, Y. R., Wang, S., & Smith, M. A. (2020). Implicit adaptation compensates for erratic explicit strategy in human
 motor learning. *Nature Neuroscience*, 23(3), 443–455.
- Morehead, J. R., Qasim, S. E., Crossley, M. J., & Ivry, R. (2015). Savings upon Re-Aiming in Visuomotor Adaptation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 35(42), 14386–14396.
- Morehead, J. R., Taylor, J. A., Parvin, D. E., & Ivry, R. B. (2017). Characteristics of Implicit Sensorimotor Adaptation
 Revealed by Task-irrelevant Clamped Feedback. *Journal of Cognitive Neuroscience*, *29*(6), 1061–1074.
- Paolacci, G., & Chandler, J. (2014). Inside the Turk: Understanding Mechanical Turk as a Participant Pool. *Current Directions in Psychological Science*, 23(3), 184–188.
- Ranjan, T., & Smith, M. (2020, October 21). *Implicit motor adaptation is driven by motor performance prediction error rather than sensory prediction error*. Presented at the Motor Control and Motor Learning.
- Roemmich, R. T., & Bastian, A. J. (2018). Closing the Loop: From Motor Neuroscience to Neurorehabilitation. *Annual Review of Neuroscience*, *41*, 415–429.
- Schmidt, R. A., & Young, D. E. (1987). Transfer of movement control in motor skill learning. *Transfer of Learning: Contemporary Research and Applications.*, 281, 47–79.
- Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory prediction, and adaptation in motor control.
 Annual Review of Neuroscience, *33*, 89–108.

- 563 Smith, M. A., Ghazizadeh, A., & Shadmehr, R. (2006). Interacting adaptive processes with different timescales underlie
- short-term motor learning. *PLoS Biology*, 4(6), e179.
- Takiyama, K., & Shinya, M. (2016). Development of a Portable Motor Learning Laboratory (PoMLab). *PloS One*, 11(6),
 e0157588.
- Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor
 adaptation task. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 34(8), 3023–
- 569 3032.
- Tsay, Jonathan S., Avraham, G., Kim, H. E., Parvin, D. E., Wang, Z., & Ivry, R. B. (2020). The Effect of Visual Uncertainty
 on Implicit Motor Adaptation. *Journal of Neurophysiology*. doi:10.1152/jn.00493.2020
- Tsay, Jonathan S., Kim, H. E., Parvin, D. E., Stover, A. R., & Ivry, R. B. (2020). Individual differences in proprioception
 predict the extent of implicit sensorimotor adaptation (p. 2020.10.03.324855). doi:10.1101/2020.10.03.324855
- Tsay, Jonathan S., Parvin, D. E., & Ivry, R. B. (2020). Continuous reports of sensed hand position during sensorimotor adaptation. *Journal of Neurophysiology*, *124*(4), 1122–1130.
- Tsay, Jonathan S., & Winstein, C. J. (2020). Five Features to Look for in Early-Phase Clinical Intervention Studies.
 Neurorehabilitation and Neural Repair, 1545968320975439.
- Tsay, Jonathan Sanching, Haith, A., Ivry, R., & Kim, H. (2020). *Distinct Processing of Task Error and Sensory Prediction Error during Motor Adaptation*. Presented at the Motor Learning and Motor Control.
- Tsay, Jonathan Sanching, Lee, A. S., Avraham, G., Parvin, D. E., Ho, J., Boggess, M., ... Ivry, R. (2020). OnPoint: A
 package for online experiments in motor control and motor learning. doi:10.31234/osf.io/hwmpy
- Wann, J. P., & Ibrahim, S. F. (1992). Does limb proprioception drift? *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, 91(1), 162–166.
- Wei, K., & Körding, K. (2009). Relevance of error: what drives motor adaptation? *Journal of Neurophysiology*, *101*(2),
 655–664.
- Wei, K., & Körding, K. (2010). Uncertainty of feedback and state estimation determines the speed of motor adaptation.
 Frontiers in Computational Neuroscience, 4, 11.
- Werner, S., van Aken, B. C., Hulst, T., Frens, M. A., van der Geest, J. N., Strüder, H. K., & Donchin, O. (2015). Awareness
- of sensorimotor adaptation to visual rotations of different size. *PloS One*, *10*(4), e0123321.

- 590 Yin, C., Wang, H., Wei, K., & Körding, K. P. (2019). Sensorimotor priors are effector dependent. Journal of
- *Neurophysiology*, *122*(1), 389–397.