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The Relevant Signals for Sensorimotor Adaptation in Human Reaching

by

Darius Euge Parvin

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Psychology

in the

Graduate Division

of the

University of California, Berkeley

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Abstract

The Relevant Signals for Sensorimotor Adaptation in Human Reaching

by

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Doctor of Philosophy in Psychology

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Motor control is an essential part of what makes us human. It's important for learning how to walk and talk, for professional athletes and performers, and for recovery after injury, such as being able to function independently after a stroke. Indeed, one can even argue that the ultimate function of the brain is to dynamically select and execute movements. Without being able to move, we wouldn't be able to express ourselves or affect the world around us. By improving our understanding the motor system, we may not only be able to optimize rehabilitation schedules or brain machine interfaces, but also discover general principles about how the brain is structured.

Our lack of understanding of the motor system is made apparent by the current state of robotics. Humans have a number of mechanical disadvantages compared to robots: The forces generated by our muscles are variable and subject to fatigue, and there is considerable noise and delays in the motor signals sent to our muscles as well as in the processing of sensory feedback from our movements. Despite these challenges, we can perform complex and dexterous tasks, controlling our legs and body to walk along highly variable surfaces or our hands to crack an egg, tasks we do far more gracefully than the most sophisticated robots. Computers can easily outperform humans in games like chess where there are well defined rules and objectives, however, when it comes to learning new movements, it's unclear what to optimize for. What makes humans great at learning and performing movements is likely not to do with our muscles or processing power, but the learning rules instantiated in our brains.

Human motor learning is thought to be comprised of multiple learning processes. Consider a child learning to tie her shoes: The initial step involves declaratively learning a specific sequence of steps. Through trial and error, reinforcement learning would help favor certain actions over other possible actions. And sensorimotor adaptation can fine-tune the movements, allowing the child to accomplish the task for laces of different thickness or when wearing gloves on a wintry day. These different processes are thought to rely on different brain regions, and the extent to which they are independent processes or interact with each other is an open question.

In order to move accurately throughout life, the motor system must compensate for changes in the body and environment. Sensorimotor adaptation refers to the automatic and implicit process, one this is dependent on the integrity of the cerebellum, essential for keeping the sensorimotor system calibrated. For this form of supervised learning, the actual sensory feedback is compared to the predicted sensory consequences of a movement, with the difference constituting a sensory prediction error. The sensory prediction error is used to make rapid adjustments in an on-going

movement and as a learning signal to alter the next movement in order to reduce the movement error.

A key insight concerning sensorimotor adaptation is that this process appears to be impervious to task goals. In a seminal study, Mazzoni and Krakauer (2006) perturbed the visual feedback while participants performed a reaching task. By providing instructions about the perturbation, the participants were able to immediately adjust their behavior such that the cursor hit the target. However, the adaptation system continued to respond to the mismatch between the predicted and observed limb position, even though in this context, the consequences of adaptation were actually detrimental to task performance. This conclusion has been reinforced with a number of different tasks over the past decade, underscoring the automatic nature of adaptation and, computationally, that this learning process is concerned with ensuring that a selected movement is executed properly, rather than that the selected movement is appropriate.

This body of work raises the question of the constraints on adaptation: If not task performance, what sources of feedback influence adaptation? The central purpose of this thesis is to characterize the features of sensory feedback that influence sensorimotor adaptation. By understanding the relevant features or inputs that constrain adaptation, we may be able to better understand the information that is communicated to this learning process. From these we could hypothesize how brain regions involved in adaptation interact with other brain regions that contribute to motor control. This should also lead to new insights and testable predictions about how the motor system will respond in various situations, meaning we could design more effective learning environments where these features are pronounced. In this thesis, I study the inputs to sensorimotor adaptation by testing cases with multiple or ambiguous sources of feedback, exploring how these signals affect performance.

In Chapter 1, I investigate the potential interaction between sensory prediction errors and reward prediction errors. To study this, I use a task in which participants reach towards targets in order to earn points. I manipulate both the task feedback (reward or no reward) and movement feedback, asking how these different feedback signals interact with each other. Contrary to previous hypotheses, we find that sensorimotor adaptation and reinforcement learning operate in parallel. Furthermore, I show that a key feature determining choice behavior is a sense of agency: Does the participant believe they have control over the outcome. If so, they are more likely to seek higher payoffs (riskier behavior) compared to when they believe that they do not control the outcome.

In Chapter 2, I present multiple feedback signals linked to a single movement. By varying which sources of feedback are task relevant and which are task-irrelevant, I ask if adaptation is sensitive to task relevance (even if insensitive to task outcome). The alternative hypothesis is that all feedback information is treated in a similar manner by the adaptation system. The results show that the adaptation system is sensitive to task relevance. However, overall adaptation is attenuated in the presence of irrelevant feedback signals. These results highlight a novel role of task relevance for sensorimotor adaptation, particularly in situations with multiple or redundant sources of feedback.

In Chapter 3, I explore the interaction of vision and proprioception in sensorimotor adaptation. Previous experiments have shown that adaptation in response to visual errors has a limited capacity; the system can be recalibrated up a certain point, beyond which accurate performance requires some sort of change in the movement plan. The basis for this limited capacity is unclear. One hypothesis is that the upper bound on adaptation reflects an equilibrium point between signals

concerning visual and proprioceptive sensory prediction errors. This hypothesis predicts that, as proprioceptive information becomes less reliable, the sensitivity to visual errors should be relatively greater, and thus produce a larger upper bound on adaptation. I test hypothesis by asking if variation across individuals in terms of their sensitivity to proprioception is predictive of their response to a visual perturbation. The results show a negative correlation between proprioceptive acuity and the magnitude of adaptation to a visual error, consistent with the idea that adaptation entails the integration of different sensory prediction error signals.

In summary, by studying the response of adaptation of multiple sources of feedback, we have furthered our understanding of the constraints on sensorimotor adaptation. We find that sensorimotor adaptation not only integrates feedback from vision and proprioception, but that under situations it is also sensitive to the task relevance. Although we did not find evidence for a direct interaction between adaptation and decision making, our finding of adaptation's sensitivity to task relevance suggests an exciting possibility for the interaction with other goal directed systems.

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Contributions

I would like to thank my co-authors. Their contributions are listed below:

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Chapter 2 - Darius E. Parvin, J. Ryan Morehead, Kristy V. Dang, Alissa R. Stover, Richard B. Ivry

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Contents

Chapter 1 - Credit assignment in a motor decision making task is influenced by agency and not sensorimotor prediction errors.....	1
Abstract.....	1
Introduction.....	1
Materials and Methods.....	2
Results.....	8
Discussion.....	15
Chapter 2 - Implicit adaptation is modulated by the relevance of feedback	19
Abstract.....	19
Introduction.....	19
Methods	21
Results.....	27
Discussion.....	33
Supplementary Information	36
Chapter 3 - Individual differences in proprioceptive reliability predict the extent of implicit sensorimotor adaptation.....	37
Abstract.....	37
Introduction.....	37
Methods	39
Results.....	45
Discussion.....	52
References	53

Chapter 1

Credit assignment in a motor decision making task is influenced by agency and not sensorimotor prediction errors

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Abstract

Failures to obtain reward can occur from errors in action selection or action execution. Recently, we observed marked differences in choice behavior when the failure to obtain a reward was attributed to errors in action execution compared to errors in action selection (McDougle et al., 2016). Specifically, participants appeared to solve this credit assignment problem by discounting outcomes in which the absence of reward was attributed to errors in action execution. Building on recent evidence indicating relatively direct communication between the cerebellum and basal ganglia, we hypothesized that cerebellar-dependent sensory-prediction errors (SPEs), a signal indicating execution failure, could attenuate value updating within a basal-ganglia dependent reinforcement learning system. Here we compared the SPE hypothesis to an alternative, “top-down” hypothesis in which changes in choice behavior reflect participants’ sense of agency. In two experiments with male and female human participants, we manipulated the strength of SPEs, along with the participants’ sense of agency in the second experiment. The results showed that, whereas the strength of SPE had no effect on choice behavior, participants were much more likely to discount the absence of rewards under conditions in which they believed the reward outcome depended on their ability to produce accurate movements. These results provide strong evidence that SPEs do not directly influence reinforcement learning. Instead, a participant’s sense of agency appears to play a significant role in modulating choice behavior when unexpected outcomes can arise from errors in action execution.

Introduction

Consider the situation in which a tennis player attempts a passing shot, only to have her opponent easily return it with a winning volley. The player must decide if the fault lies with her choice to hit a passing shot rather than a lob, or with her poor execution of the passing shot. How the brain solves this credit assignment problem -- whether to attribute successes or failures to the selection or execution of actions -- is poorly understood.

Reinforcement learning models that incorporate variables such as reward magnitude and reward probability have been quite successful in predicting choice behavior (Rescorla and Wagner, 1972) and associated neuronal activity (Schultz et al., 1997). Missing from this equation, however, is the role of action execution. These actions introduce a new set of variables to incorporate into the

decision-making process, such as the effort required to make a particular choice (Walton et al., 2006; Hartmann et al., 2013) or the probability of successfully executing the required movement (Thrommershäuser et al., 2008; Wu et al., 2009; Landy et al., 2012). However, current models typically overlook the credit assignment problem, given the negligible role of motor errors in standard reinforcement learning tasks.

We recently considered how processes specific to action execution could provide information required to solve this problem (McDougle et al., 2016). We compared a traditional, button-pressing “bandit task” with a modified version in which participants indicated their choices by reaching to one of two targets. In the former, the absence of reward provided information about the outcome probabilities associated with each stimulus (e.g., action selection error), whereas in the latter, the absence of reward provided information about reaching inaccuracy (e.g., action execution error), indicated by a visual cursor that landed outside the target. The results showed that participants’ choice behavior was less sensitive to action execution errors compared to action selection errors. We proposed that this difference may have been due to the presence of a motor execution error signal in the reaching condition.

In the motor domain, sensory prediction errors (SPE), the discrepancy between the predicted and actual sensory feedback, are used to correct the ongoing movements or to drive motor adaptation (Wolpert et al., 1995; Tseng et al., 2007). This signal could be directly exploited by the reinforcement learning system to solve the credit assignment problem. That is, the presence of an SPE could signal that the absence of the expected outcome (negative reward prediction error, RPE), should be attributed to an error in movement execution rather than an erroneous choice. This “bottom-up” SPE hypothesis could provide a functional account of the relatively direct connections between the cerebellum, a critical component in the generation of SPEs, and the basal ganglia, parietal lobe, and orbital prefrontal cortex, core structures in reinforcement learning.

Alternatively, the credit assignment problem could be solved by a more “top-down” process related to a sense of agency, operationalized here as the belief that success or failure in obtaining a reward is determined by motor performance rather than the result of a property of the choices themselves. Green and colleagues (2010) proposed a model in which agency influences the rate of change in the values associated with response choices. In our reaching version of the bandit task, this would result in behavior consistent with discounting RPEs on trials with negative outcomes.

The current study further explores how action execution errors modulate reinforcement learning. The SPE hypothesis predicts that choice behavior should be sensitive to manipulations of the strength of the SPE, even if those manipulations are irrelevant to the reward outcomes. In contrast, the agency hypothesis predicts that manipulations of SPE strength should have a minimal effect on biases in choice behavior, and instead be influenced by the belief that the outcomes are dependent on their motor accuracy. Using a reaching variant of the two-armed-bandit task, we manipulated SPE by delaying reach feedback (experiment 1), and by using “clamped” reaching feedback (experiment 2). In experiment 2, we also manipulated the task instructions to test whether biases in choice behavior were modulated by the participants’ sense of agency.

Materials and Methods

Participants

All participants provided written consent, approved by the institutional review board at the University of California, Berkeley. All participants were right handed, based on self-report and an assessment with the Edinburgh Handedness Inventory (Oldfield, 1971). Participants received either class credit or monetary compensation.

Experimental apparatus

Participants made reaching movements with their right arm on a graphics tablet (49.3 cm by 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA, sampling rate = 200 Hz.), while holding a digitizing pen, embedded in a custom handle. The stimuli were presented on a monitor that was positioned above the tablet (53.2 cm by 30 cm, ASUS). The monitor occluded the participant's view of their hand.

Reaching task

At the start of each trial, a white circle (diameter 1.2 cm) was presented on the screen, indicating the start position (Figure 1A). The participant was instructed to move their hand to the start location. Feedback of hand position was indicated by a solid white circle (diameter 0.5 cm). This feedback was only visible when the hand was within 2 cm of the start position. After the cursor had been held in the start position for 1 s, two red circles (diameter 1 cm), were presented at a distance of 10 cm, displaced $+30^\circ$ and -30° relative to straight ahead. The word "Go" appeared in the middle of the screen, instructing the participant to reach to one of the two circles. The participant was instructed to make a slicing movement, attempting to pass through the selected target. Cursor feedback was removed once the movement was initiated. If the reach amplitude did not reach 10 cm within 1.5 s, the message "Please Reach Faster" was displayed and the trial was terminated. If the participant's reach deviated too far from either target (angular error greater than 20°), the message "Out of Bounds" was displayed. In both cases, the trial was immediately repeated.

If the hand passed within 20° of the target, one of two trial outcomes occurred. On rewarded trials, the target color changed to green, a pleasant "ding" sound was played, and the number of points earned (1-100) was displayed above the chosen target. On unrewarded trials, the target remained red, an unpleasant "buzz" sound was played, and the number "0" was displayed above the chosen target. A box on the top of the screen showed the cumulative total of points earned.

Reward Schedule

In order to assess target choice preference independent of reaching accuracy, the reward schedules were predetermined; as such, the outcomes were not contingent on whether or not the reaching movement actually intersected the selected target (with the exception of reaches judged to be out of bounds). Hit probability and reward functions were created using a bounded pseudo-sinusoidal function (Figure 1B). These functions were mirrored for each target, such that the expected value for each target on a given trial was matched. For example, a "safe" target with a 90% hit probability and reward value of 10 points would be paired with a matching risky target that had a 10% hit probability and rewarded 90 points. Note that we operationally define risk in terms of the

probability of hitting the target. On hit trials, the participant received the associated reward value for that trial; on miss trials, no points were awarded. The probability and reward functions were designed so that at multiple points during the experiment, payoffs between the left and right targets gradually shifted, allowing us to track the participant's choice preferences. The same reward schedule was used for all participants, with the position of the targets counterbalanced.

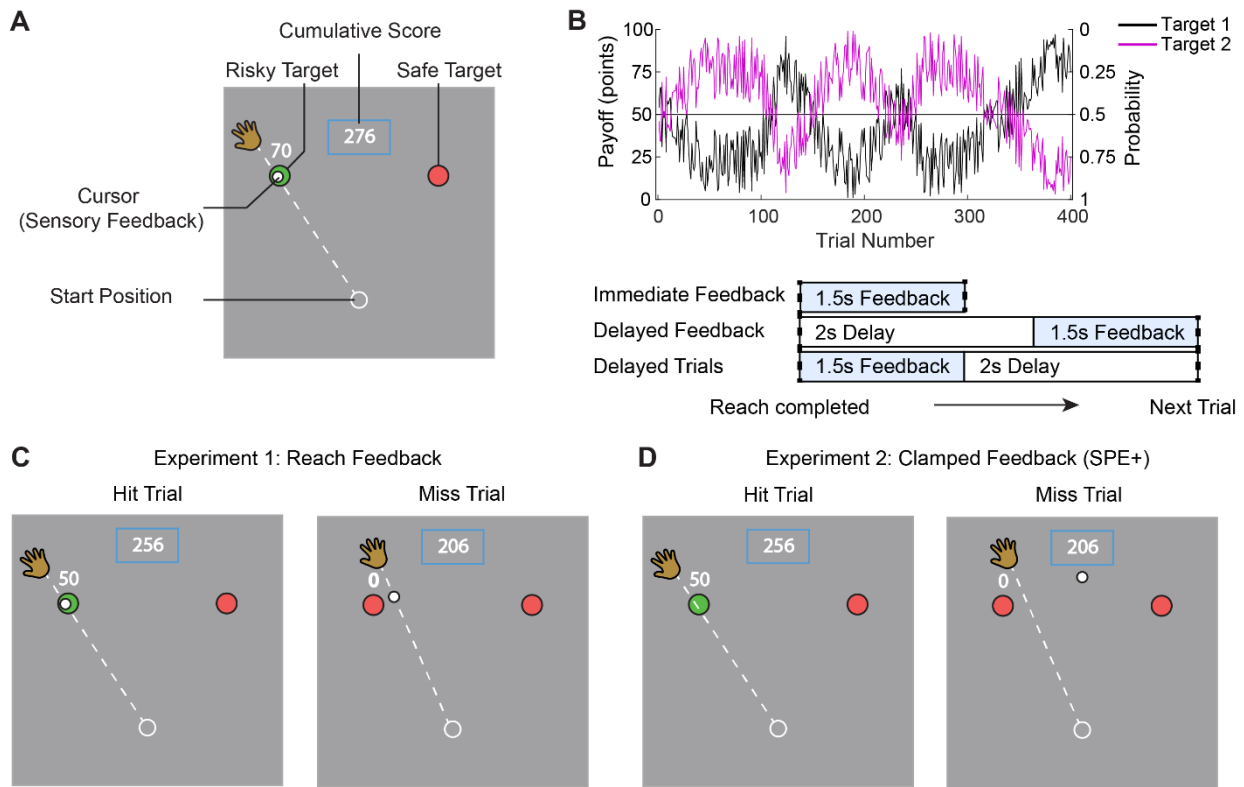


Figure 1.1. Experimental Design. A. Trials began with participants moving their hand to place the cursor at the start position. They indicated their choice preference by performing a shooting movement through the selected target. Visual feedback of the hand position was extinguished once the hand left the start position. In experiment 1, visual feedback of the reach was provided on an imaginary circle with a radius equal to the target distance. On hit trials, the target would turn green and a pleasant “ding” sound was generated. On miss trials, the target would remain red and an unpleasant “buzz” sound was generated. The number of points earned was displayed above the chosen target (“0” in the case of a miss), along with a cumulative total of points earned displayed in a box. B. Top: Reward functions (left axis) and hit probabilities (right axis) for each target. Over trials, the targets vary in terms of their relative “risk” (e.g., high payoff but low hit probability), but are always matched in terms of the expected payoff. Bottom: Three groups were tested with different feedback delays and intertrial intervals. Immediate Feedback and Delayed Trials both received immediate reach feedback. Delayed Feedback received the same reach feedback but after a 2 second delay. C. Example feedback for hit and miss trials in experiment 1. Veridical feedback was provided when participants’ actual accuracy (hit or miss) matched the predetermined outcome. For trials where they did not match, the cursor would be bumped in or out of the target on the same side, such that participants were not aware of the perturbation. D. In experiment 2, feedback of reaching accuracy was not provided. On miss trials, the feedback cursor was “clamped” and always presented at the same location between the two targets (regardless of which was chosen). On hit trials, no feedback cursor was presented.

Experiment 1

Experiment 1 was designed to compare conditions in which reach errors were signaled by a strong or weak SPE ($n = 20$ per group; total $n = 60$, 33 female, age range 18 - 25). At the location where the movement amplitude reached 10 cm, the cursor reappeared, providing the participant with a feedback signal that indicated the accuracy of the reach (Figure 1C). Presuming that the participant had intended to hit the target, the difference between the center of the target and the cursor position indicated the SPE for that trial.

Given that the hit/miss outcomes were predetermined, it was necessary to alter the feedback on some of the trials. On trials where the reach outcome matched the predetermined outcome, the reach feedback was veridical: The feedback cursor would fall on the target on hit trials (22.5% of all trials) and off the target on miss trials (27.5% of all trials). On trials where the reach outcome and predetermined outcome did not match, the reach feedback was manipulated. For “hits” that had to be converted to “misses” (25.5% of all trials), the cursor was displayed at a new location away from the target (in the same direction as the side of the target that was hit). To mask the fact that the feedback was sometimes altered, the distribution of the altered feedback signals was designed to closely match the distribution that results from variability in reaching, as determined in a pilot study (Figure 2A). The new cursor location was randomly selected from one side of a normal distribution with a SD of 4.65° , with the peak centered on the edge of the target. Locations deviating further than two times the distribution’s SD (9.3°) were resampled. For “misses” converted to “hits” (24.6% of all trials), the cursor was displayed within the target according to a uniform random distribution, but restricted to the same side as the original miss. We included the “Out of Bounds” criteria to ensure that the feedback perturbations were relatively small, and thus prevent the participants from becoming aware of the feedback manipulation.

To manipulate the strength of the SPE signal, we varied the interval between the end of the reach and the time at which cursor feedback was provided. Previous studies have demonstrated that delaying sensory feedback by over 1 s can strongly attenuate the strength of an SPE (Held et al., 1966; Kitazawa et al., 1995; Honda et al., 2012; Brudner et al., 2016; Schween and Hegele, 2017). In the Immediate Feedback group, the cursor reappeared as soon as the reach amplitude exceeded 10 cm (Figure 1B). In the Delayed Feedback group, the cursor feedback was presented after a 2 s delay. Note that this manipulation confounds feedback delays and the time between successive trials. To unconfound these factors, we also tested a third group who received immediate cursor feedback, but then had to wait an additional 2 s before the start of the next trial (Delayed Trials).

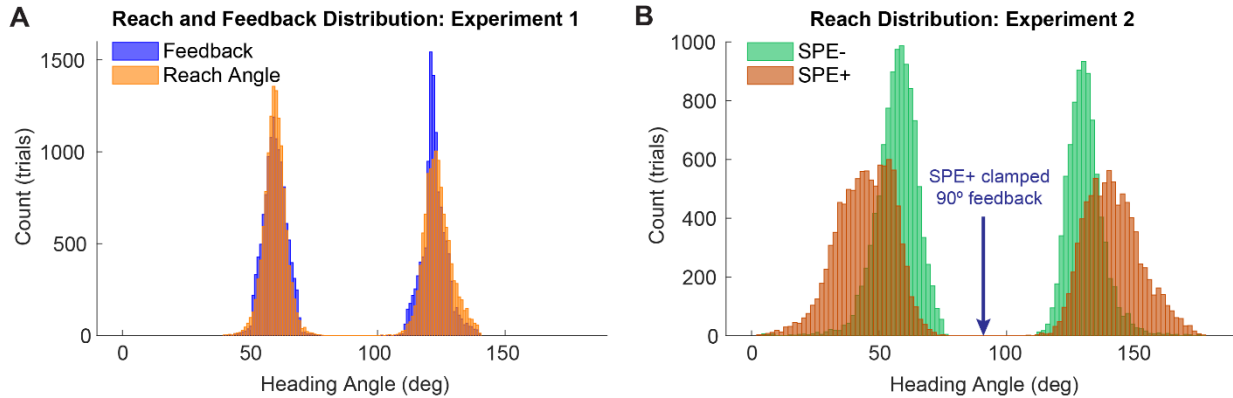


Figure 1.2 Distribution of reach endpoints and feedback location. A. In experiment 1, reach feedback was minimally altered in order to match the predetermined reward schedule. B. In experiment 2, clamped feedback was provided at an invariant location (90°) on miss trials for the SPE+ condition. As a result, the SPE+ group heading angles are shifted away from the center relative to the SPE- group, due to implicit adaptation.

Experiment 2

In experiment 2 we used a 2×2 factorial design ($n = 20$ per group; total $n = 80$, 51 female, age range 18 - 25). The first factor was to test whether an explicit sense of agency would alter participants' choice behavior. The second was to provide a second test of the SPE gating hypothesis.

In our previous study, we found no effect of agency (McDougle et al., 2016); however, our manipulation, which involved instructing participants that they were either in control or not in control of the hit/miss outcomes, may have been complicated by the inclusion of reach feedback in the vicinity of the target. The reach feedback may have unintentionally swayed participants to believe that they were still in control, regardless of the instructions. Here, we avoided this conflict by removing reach feedback completely. To manipulate a sense of agency, the participants were told that miss trials were either related or not related to their reaching accuracy. In the former case, the participants were told that the trial outcome reflected whether their reach accurately intersected the chosen target (Agency+). In the latter case, the participants were told that the outcome reflected a probability that a target choice would result in a payoff, independent of their reaching accuracy (Agency-). Beyond this instruction, the participants were not informed about the nature of the hit probabilities or reward schedule.

We also sought a second test of the SPE gating hypothesis, comparing conditions which did or did not include SPEs on miss trials. For participants in the SPE+ conditions, we used a variant of task irrelevant clamped feedback (Morehead et al., 2017; Kim et al., 2018) to elicit SPEs without conveying reaching performance: On miss trials, the cursor feedback was always presented at a common location positioned between the two targets (90°) (Figure 1D), appearing as soon as the reach amplitude exceeded 10 cm. The participants were fully informed that, regardless of which target was selected, the feedback would always appear straight ahead on unrewarded trials. Given the instructions and lack of spatial correlation between the feedback and reaching movement (Figure 2B), we assumed that these participants would not confuse the clamped feedback as

indicative of their reach angle. Nonetheless, based on our previous work with clamped feedback of this sort, we assumed that these conditions would be sufficient to elicit SPE-dependent adaptation and in fact, confirmed this in a separate “Clamp-only” control experiment (see “Clamp-only” experiment below).

Participants in the SPE+ conditions received clamped feedback on all miss trials. This feedback signal was not presented to participants in the SPE- conditions. Neither group received cursor feedback on hit trials.

Experiment 2 block structure

The experiment consisted of 30 baseline trials, 400 decision making trials, and 30 aftereffect trials. The 400 decision making trials had the same reward schedule as experiment 1. For the baseline and aftereffect trials, only one of the two targets were presented on each trial (location randomized) and the participant was instructed to reach to the target. A “ding” indicated that the movement amplitude had exceeded 10 cm. No information was provided concerning reaching accuracy.

The baseline and aftereffect trials were included to assess if the clamped feedback was treated by the motor system as an SPE. If so, the heading direction in the aftereffect block should be shifted in the lateral direction compared to the baseline block. Visuomotor adaptation was operationalized as a shift in heading angle in the aftereffect trials relative to baseline. The heading angle was defined as the angle between the hand position when it crossed the target radius, the start position, and the target. The heading angle values for the 60° target (to the right) were flipped, such that for both targets, a positive heading angle represented the angle in the direction of expected adaptation (in the opposite direction to the clamped feedback). All reported aftereffects were baseline subtracted, where the baseline was defined as the mean of all baseline trials.

Clamp-only experiment

The design and logic of experiment 2 rests on the assumption that the clamped visual feedback is treated as an SPE (Morehead et al., 2017; Kim et al., 2018). Although the comparison of the baseline and aftereffect blocks in experiment 2 provides a test of this assumption, we thought it prudent to conduct a clamp-only experiment that employed a more traditional sensorimotor adaptation design, one in which the participants did not have to choose the reach target.

Reaches were made to a single target, displayed at either 60° or 120°, the locations used in experiments 1 and 2 (Figure 4A). The experiment consisted of 30 baseline trials (15/target) in which no visual feedback was provided, 120 “clamp” trials (60/target), and 10 aftereffect trials (5/target), again with no visual feedback. The trial structure was the same as in the baseline and aftereffects blocks of experiment 2.

The clamp-only experiment also provided an opportunity to test the effect of delayed visual feedback on sensorimotor adaptation, relevant to our manipulation in experiment 1. Two groups were tested (14/group, 14 female, age range 18 - 25), one in which the clamped feedback was provided coincidentally with the reach endpoint (“No Delay”), and a second in which the feedback was delayed by 2 s (“Delay”). If the clamp is treated as an SPE, adaptation should be evident in the “No Delay” group and abolished, or severely attenuated in the “Delay” group.

Statistical Analysis

The chosen sample sizes were based on our previous studies using the reaching variant of the two-armed bandit (McDougle et al., 2016) and the clamp method (Morehead et al., 2017; Kim et al., 2018). All t-tests were two-tailed and used a threshold for significance (alpha) of 0.05 unless stated otherwise. We computed the inverse Bayes-factor (BF01) for our results from experiment 1 in order to assess the likelihood of the null hypothesis (H0) relative to the SPE hypothesis (H1). We used a method proposed by Rouder et al. (Rouder et al., 2009), using a prior for effect size following a Cauchy distribution with a scale factor of 1. Here, $BF01 < 1/3$ can be considered as strong evidence in favor of the alternative hypothesis, $BF01 > 3$ as strong evidence in favor of the null hypothesis, and anything between is only considered weak or anecdotal (Dienes, 2014).

Results

Experiment 1

In experiment 1, we set out to test the SPE gating hypothesis, the idea that the operation of the reinforcement learning system is attenuated following trials in which the absence of a reward is attributed to an error in action execution rather than action selection. The core prediction of this bottom-up hypothesis is that the strength of the SPE signal should influence choice behavior. Participants were tested in a two-armed bandit task, indicating their choices on each trial by reaching to one of two targets. In addition to receiving reward feedback, cursor feedback indicated the accuracy of the reach. We compared two groups, an Immediate Feedback group who saw the feedback cursor immediately at the end of the reach and a Delayed Feedback group, for whom the appearance of the feedback cursor was delayed by 2 s. Based on previous studies, the strength, or salience of SPE should be considerably attenuated in the Delayed Feedback group (Held et al., 1966; Kitazawa et al., 1995; Honda et al., 2012; Brudner et al., 2016; Schween and Hegele, 2017). Given that the 2 s feedback delay also increases the time between successive trials, we also tested a Delayed Trials group in which the feedback cursor appeared immediately at the end of the reach, but with an extra 2 s pause between trials. In this manner, we matched the trial-to-trial interval of the Delayed Feedback and Delayed Trials groups.

In standard bandit tasks in which the outcome is not dependent on action execution, people typically show a preference for the “safe” target, consistent with a risk aversion bias (Kahneman and Tversky, 1979; Niv et al., 2012; McDougle et al., 2016). In a previous study (McDougle et al., 2016; see also, Wu et al., 2009), we observed a striking reversal of this preference when the choices were indicated by reaches, so that the failure to obtain a reward was attributed to a failure of action execution. The SPE gating hypothesis predicts that this reversal is due to the presence of SPEs on miss trials. Consistent with those results, the Immediate Feedback group and Delayed Trials group showed a consistent preference for the riskier target over the course of the experiment (Figure 3a). However, in contrast to the SPE hypothesis, the Delayed Feedback group also showed a reversal of the risk aversion bias, even though we assume the strength of the SPE is greatly attenuated by the delay (an assumption we confirm in experiment 2).

For each trial, we defined the risky target as the one with the lower hit probability, but higher payoff, and as such the option with a larger variance of potential outcomes (Kahneman and Tversky, 1979; Caraco et al., 1980; Dayan and Niv, 2008; Schultz, 2016). Using this definition, we quantified participants' choice biases by calculating the ratio of trials in which they picked the riskier target over the total number of trials (excluding the few out of bounds trials). A one-way ANOVA revealed a significant effect of Group on risk bias, ($F(2,57) = 4.65, p = 0.01$; Figure 3B).

Post hoc t-tests using Bonferroni-adjusted alpha levels of 0.017 ($.05/3$) were conducted. A numerical but non-significant difference (after correcting for multiple comparisons) existed between the Immediate Feedback and Delayed Feedback groups ($t(38) = 2.13, p = 0.04$). This difference is in a direction consistent with the hypothesis that SPE influences choice behavior. However, we observed a significant difference between the Immediate Feedback and Delayed Trials groups ($t(38) = 2.95, p = 0.005$), indicating that an increase in intertrial interval alone (i.e. without manipulating the SPE) affected choice preference. The Delayed Feedback group had a numerically lower risk bias compared to the Delayed Trials group, opposite to what the SPE hypothesis predicts, although this difference was non-significant ($t(38) = 0.93, p = 0.36$). An inverse Bayes-factor comparing the odds of the hypothesis that the Delayed Feedback and Delayed Trials risk biases were equal (null) versus the hypothesis that they were unequal provided only weak support in favor of the null ($BF_{01} = 2.95$).

Together, these results fail to support the hypothesis that choice biases are modulated by the strength of the SPE. The most parsimonious interpretation of the current results is that choice biases in the current task decay as a function of the time between successive trials, independent of the strength of the SPE. This could be the result of time-sensitive processes such as a decay of the representations of the value of the target, or decay of a motor memory that could be used to adjust the next movement (see Discussion).

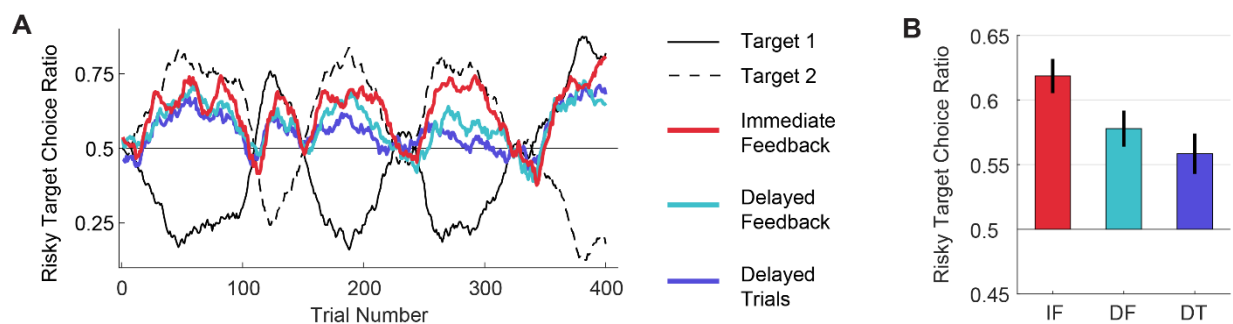


Figure 1.2 Increasing the trial-to-trial interval, either by delaying feedback or increasing the intertrial interval resulted in a preference for the risky target. A) Mean group choice behavior reveals overall preference for riskier target throughout the experiment. The colored lines represent the proportion of choices made to the riskier target, averaged over participants in each condition (calculated over a 15-trial window moving average). The relative “riskiness” of target 1 and target 2 (determined by the predefined reward schedule) are shown for illustrative purposes (black solid and dashed lines). B) Risk preference quantified as the ratio of trials where the riskier target was chosen over the total number of trials. All groups exhibited a preference for the riskier choice ($>.50$), with this effect significantly greater for the IF group compared to the other two. IF: Immediate Feedback, DF: Delayed Feedback, DT: Delayed Trials. Error bars represent ± 1 SEM over participants.

Experiment 2

The results of the first experiment indicate that SPE is not a critical signal that directly modulates choice biases. An alternative hypothesis is that, due to the sense of agency associated with reaching (Green et al., 2010), people may be slow to update their estimates of action execution errors based on recent outcomes. For example, the participants have a strong prior for their reaching competency and believe that their execution errors simply reflect motor noise, a variable which should operate randomly across trials. We set out to test this hypothesis in experiment 2, comparing conditions in which participants were told that the absence of reward was attributed to a failure in motor execution (Agency+) to conditions in which the absence of reward was attributed to a property of the object (Agency-). If the sense of agency is critical, we would expect participants to prefer the “safe” target in the latter conditions.

We also designed experiment 2 to provide a second test of the SPE hypothesis. To that end, we compared conditions in which the trial outcome included clamped cursor feedback (SPE+) or did not include this feedback (SPE-). This feedback, when provided, was always presented at the same location midway between the two targets, independent of their target choice. Based on previous work with clamped feedback (Morehead et al., 2017; Kim et al., 2018), we assumed that this signal would automatically be treated by the motor system as an SPE, driving sensorimotor adaptation. However, given the results of experiment 1, we expected that the presence or absence of SPE would not influence choice behavior.

We first verified that clamped feedback, even if only presented at the end of the movement, was sufficient to produce adaptation (see Methods, Clamp-Only Experiment). Despite being informed about the nature of the clamped feedback and instructed to ignore it, robust adaptation was observed when the clamped feedback was presented: During the clamp block, the heading angle for each target shifted in the opposite direction of the cursor and an aftereffect was observed (Figure 4B). A t-test of the baseline-subtracted final heading angle revealed the aftereffect being significantly greater than 0 ($t(13) = 4.65$, $p < 0.001$). Moreover, these effects were absent if the feedback was delayed by 2 s ($t(13) = -0.19$, $p = 0.85$), providing further evidence that this type of feedback is treated like an SPE by the motor system and causes robust implicit learning (Held et al., 1966; Kitazawa et al., 1995; Honda et al., 2012; Brudner et al., 2016; Schween and Hegele, 2017).

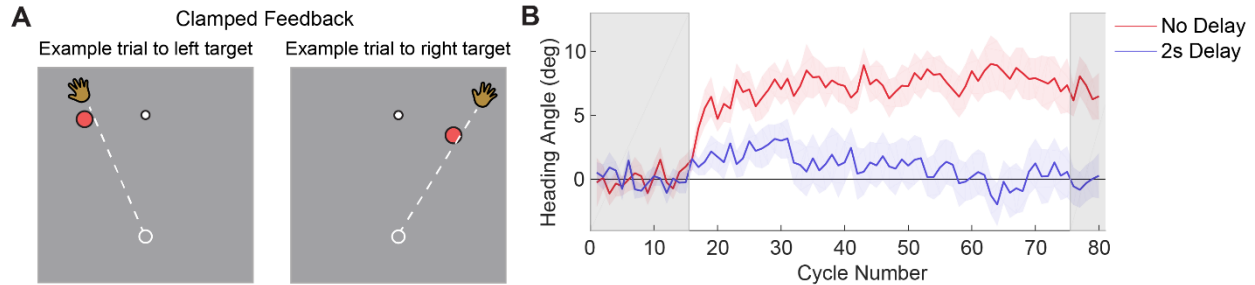


Figure 1.4 Clamped Feedback experiment showing sensorimotor adaptation from clamped feedback, but only if the feedback is immediate. A) Participants were instructed to reach toward the single target. Clamped feedback would always appear straight ahead at the end of the reach, regardless of the participant’s heading angle. B) Immediate clamped feedback (“No Delay”) elicits a significant aftereffect in the expected direction for both targets. No aftereffect is observed when the clamped feedback is delayed by 2s (“2s Delay”). Lines represent mean hand angle over participants and shaded regions around the lines represent ± 1 SEM over participants. Grey regions represent baseline and aftereffect trials where one target was presented at a time and with no reach feedback.

Adaptation also occurred in response to the clamped feedback in the main experiment. During the choice trials, heading angle again shifted in the opposite direction of the cursor (Figure 5A), and there was a pronounced aftereffect (Figure 5B). (Note that such an accumulation of adaptation leading to an aftereffect would not occur in experiment 1, as errors were presented on both sides for each target.) These effects were not observed for the groups in which the cursor was never presented. A two-way ANOVA comparing the heading angle in the aftereffect block to the baseline block revealed a main effect of SPE ($F(1,76) = 40.7, p < 0.001$), but no effect of agency ($F(1,76) = 1.05, p = 0.31$), nor an interaction ($F(1,76) = 0.38, p = 0.54$). We note that the magnitude of the adaptation was numerically larger for the SPE group who were told they controlled the trial outcome. While this may indicate that adaptation is influenced by a sense of agency, the participants in the Agency+ group chose the risky target more often (see below), experienced more “miss trials”, and thus received more SPEs.

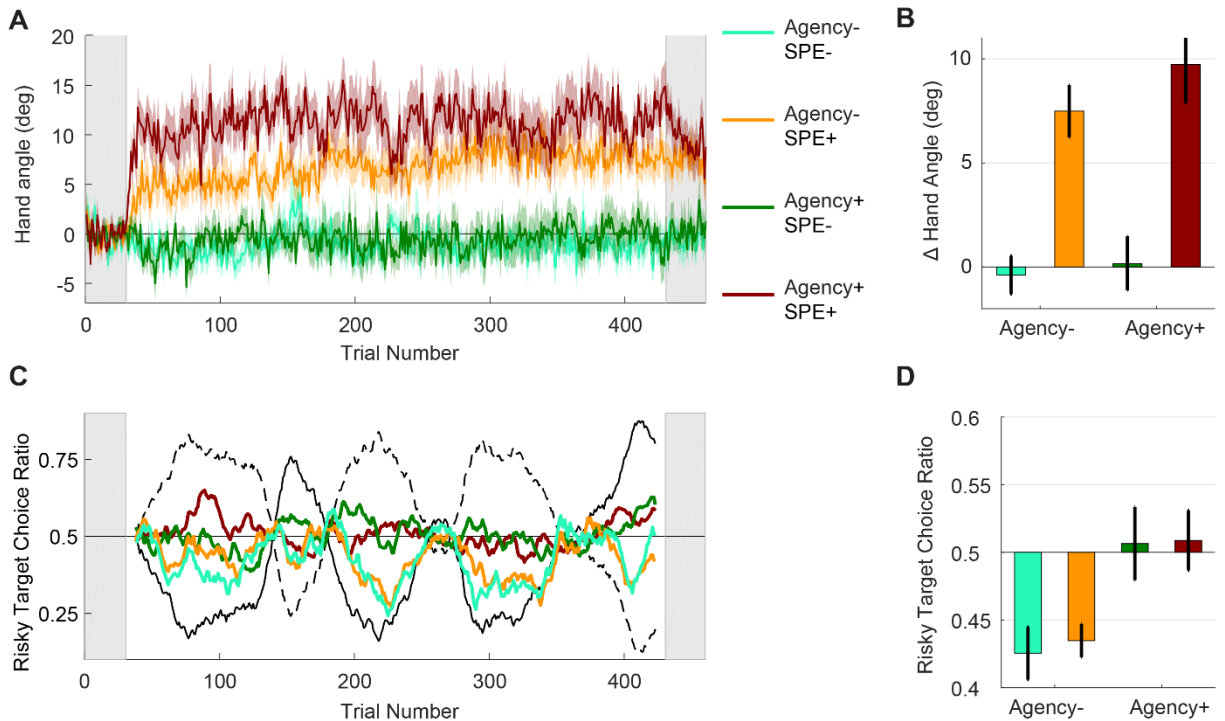


Figure 1.5 Sense of control, but not presence of SPE, influences choice preference. A) Heading angle of reaches reveals the time course of adaptation. Hand angles for the 45° target are flipped such that positive is in the direction of adaptation. Lines represent mean hand angle over participants and shaded regions around the lines represent ± 1 SEM over participants. Grey regions represent baseline and aftereffect trials where only one target was presented and no reach feedback was provided. B) Baseline-subtracted aftereffects show significant adaptation for both SPE+ conditions, and none for the SPE- conditions. C) Group averaged choice behavior shows a bias toward the safe target for the Agency- conditions, and no bias for Agency+ conditions. The colored lines represent the proportion of choices made to the riskier target, averaged over participants in each condition (calculated over a 15-trial window moving average). The relative “riskiness” of target 1 and target 2 (determined by the predefined reward schedule) are shown for illustrative purposes (black solid and dashed lines). D) Choice bias is influenced by a sense of control, rather than SPE.

Having established that the clamped feedback was an effective SPE, we next asked if choice behavior was influenced by the presence of an SPE, a sense of agency, or an interaction of these variables. When participants were led to believe that the absence of reward was due to an action execution error, they did not show the same risk averse (“safe”) bias compared to when they were told that the absence of reward reflected a probabilistic property of the target. As can be seen in Figure 5 C&D, the Agency- groups tracked the “safe” target, whereas the Agency+ groups showed no consistent bias in their choice behavior. In contrast, the presence of an SPE had no influence on choice behavior. A two-way ANOVA showed a main effect of agency ($F(1,76) = 13.83$, $p < 0.001$), but not feedback type ($F(1,76) = 0.08$, $p = 0.78$), and there was no interaction between these variables ($F(1,76) = 0.03$, $p = 0.87$).

In summary, the results of experiment 2 indicate that the presence of SPE, while leading to adaptation, is not sufficient to influence decision making. In contrast, variation in the sense of

agency did influence choice behavior, with participants more likely to choose the risky target when they believed they were in control, at least to some degree, of the trial outcome.

Model-based analysis of the agency hypothesis

Experiment 2 was designed to examine if choice behavior is affected when a sense of agency is explicitly manipulated, operationalized as the belief that outcomes are the result of motor performance. We hypothesized that a sense of agency would influence behavior by reducing the influence of temporal dependency of trial outcomes (see Green et al., 2010). Specifically, if motor errors are assumed to reflect random noise in the Agency+ conditions, recent hits and misses would not be informative about future hits and misses. In contrast, hit and miss outcomes are independent of the agent's motor accuracy in the Agency- conditions; thus, recent outcomes should provide useful information about future outcomes.

To evaluate whether this agency hypothesis could account for our observed behavior in experiment 2, we developed a reinforcement learning model to capture how temporal dependency could influence choice behavior. In this model, the estimated hit probabilities $\hat{p}_t(x)$ and payoffs $E_t(x)$ for each target x on trial t are updated on a trial-by-trial basis, based on the differences between the actual and predicted outcomes (see McDougale et al., 2016). The degree of temporal dependence is captured by two learning rate parameters, α_{prob} and α_{payoff} , that correspond to the proportion that these estimates are updated based on the previous trial outcome:

$$\delta_{\text{prob},t} = r_t^* - \hat{p}_t(x)$$

$$\delta_{\text{payoff},t} = r_t - E_t(x)$$

$$\hat{p}_{t+1}(x) = \hat{p}_t(x) + \alpha_{\text{prob}} \delta_{\text{prob},t}$$

$$E_{t+1}(x|\text{hit}) = E_t(x) + \alpha_{\text{payoff}} \delta_{\text{payoff},t}$$

$$V_{t+1}(x|\text{hit}) = \hat{p}_{t+1}(x)E_{t+1}(x)$$

where $\hat{p}_t(x)$ takes on a value between 0 and 1 for each target, representing the probability that a reach to that target will result in a hit. The hit or miss outcome (independent of reward), r^* , is coded as a 1 or 0 for a hit or a miss, respectively. Differences between the estimated hit probability and the actual outcome $\delta_{\text{prob},t}$, are multiplied by α_{payoff} and added to the estimated hit probability for the next trial. As a result, α_{prob} captures the degree to which a participant updates the estimates of hit probability as a result of previous trials. By fitting α_{prob} as a free parameter for each participant, we can estimate the degree to which they behaved as though they believed the hit outcomes were temporally dependent, with higher values representing stronger temporal dependence. If participants treat motor execution errors as temporally independent when they believe the outcomes are dependent on their reaching accuracy (Agency+ groups), we should

observe lower α_{prob} compared to when they believe the outcomes are not dependent on reaching accuracy (Agency- groups).

Estimated payoffs were updated in a similar manner to estimated probabilities. However, for payoffs, r takes on values from 1-100 according to the observed payoff, and the update only occurs following hit trials. This conditional is a central component of the model, as it effectively separates trials in which outcomes are due to motor errors from trials that result in standard reward prediction errors. α_{payoff} is fit as a free parameter for each participant and also reflects the degree of temporal dependence in payoffs. Since the payoff amounts were not dependent on hit accuracy, but rather a property of the target, we expected α_{payoff} to be approximately constant across all the experimental conditions.

Estimated target values $V(x)$ were transformed into probabilities using a standard softmax function. The inverse temperature parameter (τ) for the softmax was fit with one common value for all 80 participants in experiment 2, resulting in 161 free parameters in total (one α_{prob} and α_{payoff} per participant, and one common τ). Free parameter estimates were made using the `fmincon` function in Matlab, which minimized the negative log likelihood of the choices for the parameters. The learning rates (α_{prob} and α_{payoff}) were bounded between 0 and 1, and the inverse temperature parameter (τ) was bounded between 0.05 and 10.

We fit the learning parameters, then generated choice data to simulate risk preferences. The agency model was capable of simulating the pattern of behavioral risk biases observed in experiment 2 (Figure 6A). Consistent with the predictions of the agency hypothesis, the groups which were told their reaching accuracy did not influence hit probability (Agency- groups) had a higher $\alpha_{\text{probability}}$ value than the groups which were told their reaching accuracy determined the hit outcomes (Agency+ groups) (Figure 6B). A two-way ANOVA revealed a significant effect of agency on α_{prob} ($F(1,76) = 7.85$, $p = 0.01$), no effect of SPE ($F(1,76) = 1.82$, $p = 0.18$), and no interaction between the two ($F(1,76) = 0.08$, $p = 0.78$). Also consistent with the agency hypothesis, a two-way ANOVA revealed no significant effects of agency on α_{payoff} ($F(1,76) = 1.06$, $p = 0.31$), no effect of SPE ($F(1,76) = 1.93$, $p = 0.17$), and no interaction between the two ($F(1,76) = 0.16$, $p = 0.69$).

These results support the hypothesis that differences in choice behavior across groups were mainly influenced by the degree to which they treated hit probabilities as being temporally dependent, with a belief of agency leading to more temporal independence.

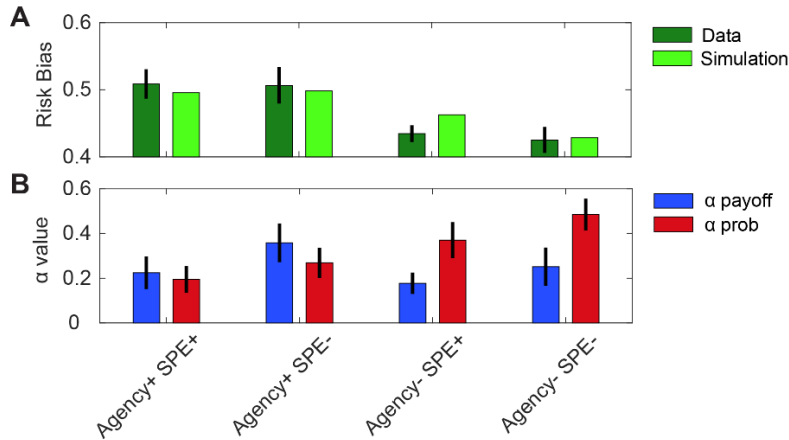


Figure 1.6 Agency model fits for experiment 2. A) Simulations based on fitted parameters produce pattern of risk biases that are similar to those observed in the four conditions of experiment 2. B) Fitted learning parameters (α payoff and α prob) for each condition. Agency+ conditions have a lower α prob than Agency- conditions, consistent with the hypothesis that participants treat hit probabilities as less temporally dependent when they have a sense of agency. Error bars represent ± 1 SEM over participants.

Discussion

People are less sensitive to unrewarded outcomes when they are attributed to errors in action execution rather than action selection (McDougle et al., 2016). The main objective of this study was to evaluate different cues that could be used to solve this credit assignment problem. In earlier work, we had proposed a bottom-up hypothesis by which cerebellar-dependent sensory-prediction errors (SPEs) were exploited by the reinforcement learning system, signaling the presence of an execution error (McDougle et al., 2016). By this model, SPEs provide a salient signal that the trial outcome should be attributed to the agent (i.e., execution error), rather than the chosen object (i.e., selection error). We tested this hypothesis in experiment 1 by manipulating the strength of SPE and in experiment 2 by presenting movement-irrelevant SPEs. In both cases, the results failed to support the hypothesis that SPE played a critical role in producing the observed bias in choice behavior. Instead, we found that the sense of agency had a significant effect on choice behavior, suggesting that the credit assignment problem may be solved in a more indirect, top-down manner.

Salience of Sensory Prediction Errors does not Influence Biases in Choice Behavior

The strongest argument against the SPE hypothesis comes from experiment 1. Here we compared conditions in which the feedback cursor was presented immediately at the end of the movement or after a 2 s delay. Previous work, as well as our clamp-only control experiment, has shown that a 2 s feedback delay strongly attenuates sensorimotor adaptation (Held et al., 1966; Kitazawa et al., 1995; Honda et al., 2012; Brudner et al., 2016; Schween and Hegele, 2017), presumably because the delay weakens the SPE. If SPE directly modulates choice preferences, then we expect participants to become more sensitive to unrewarded outcomes when the feedback was delayed.

Although this effect was observed, a similar pattern was elicited when the intertrial interval was extended by 2 s, even if the cursor feedback was immediate. Thus, the most parsimonious account of these results is that the time between successive choices, rather than SPE, decreased sensitivity to unrewarded outcomes.

Why might an increase in the intertrial interval change choice preferences? One hypothesis is that some form of iconic motor memory is strong when the interval is short (Adams and Dijkstra, 1966; Posner and Konick, 1966; Laabs, 1973; Annett, 1995; Miyamoto et al., 2014), leading the participants to believe they can correct the execution error. However, we found no evidence that participants showed a stronger adjustment in reach trajectories in the Immediate Feedback condition compared to when the feedback or intertrial interval was extended: The mean proportion of the error corrected on trials where feedback was artificially perturbed was 0.57 (standard error = 0.04) for the Immediate Feedback condition, 0.57 (0.08) for the Delayed Feedback condition and 0.53 (0.04) for the Delayed Trials conditions. A one-way ANOVA on the regression between error and change in hand angle revealed no effect of group ($F(2,57) = 0.12$, $p = 0.89$). An alternative hypothesis is that the longer intertrial interval resulted in more time discounting of the potential rewards for each target (Frederick et al., 2002). This would have the effect of attenuating all choice biases, consistent with our findings.

The results of experiment 2 provide further evidence against the SPE hypothesis. Here we used a method in which the SPE signal is not contingent on movement accuracy. Consistent with our previous work, this method was sufficient to produce adaptation in the reaching behavior of the participants. Nonetheless, choice biases were similar, regardless of whether this signal was present. Taken together, the results argue against a simple, bottom-up model in which an SPE signal is sufficient to attenuate value updates when the outcome error is attributed to a failure in motor execution.

Choice Biases are Influenced by a Sense of Agency

The results of the present study point towards a more top-down mechanism for solving the credit assignment required to differentiate execution and selection errors. This was most clearly observed in the results of experiment 2, where sensitivity to unrewarded outcomes was reduced when the instructions emphasized that the participants had some degree of agency in determining the outcome, with agency operationalized as the belief that outcomes are dependent on one's motor performance. Similarly, Green and colleagues (2010) found that choice behavior could be dramatically altered by instructing participants that the trial outcome was either determined by the computer, or contingent on movement execution. Computationally, they suggested that people assume weaker temporal dependence between successive events when the outcomes depend on motor output, given that errors from motor noise are assumed to be random. Properties of the object, however, may be more temporally dependent (e.g., the target with the high payoff on the previous trial is likely to yield a high payoff on the next trial).

In modeling the data from experiment 2, we adopted an operational definition of agency introduced by Green et al. (2010), namely that a sense of agency will cause choices to be more temporally independent. Consistent with the agency hypothesis, the fits showed that participants in conditions of high agency were less likely to behave as though hit outcomes were temporally dependent. In other words, by treating execution errors as though they were random events and unlikely to occur

again, they were more likely to choose the target with the higher expected payoff. Participants in the low agency condition, however, were more likely to behave as though misses were a property of the target, and therefore, were biased to avoid the target which resulted in more misses.

We note that in our earlier study (McDougle et al., 2016), we had included a similar manipulation of a sense of control, informing participants that the position of the feedback cursor was either dependent or independent of their movement. Contrary to the current results, we observed no effect of agency on choice behavior when an SPE-like signal was present. However, the feedback cursor still appeared near the selected target, either as veridical feedback or in a slightly shifted position. It is possible that, despite the instructions, the correlation between their movements and sensory feedback may have led the participants to believe, implicitly or explicitly, that they could control the reward outcomes. The clamped feedback used in experiment 2 avoids this problem since the feedback was spatially independent of the movement.

A similar explanation may also account for the between-experiment differences in choice behavior observed in conditions in which the participants were instructed to believe they were in control of the trial outcomes. Although the reward schedules were identical, the participants in experiment 1 exhibited a stronger bias for the risky target than the participants in experiment 2. This was verified in a post-hoc analysis, restricted to the Immediate Feedback condition in experiment 1 and the two Agency+ groups in experiment 2, ($t(58) = 4.25, p < 0.001$). The main difference between these conditions was that endpoint reach feedback was provided in experiment 1, but not experiment 2. The endpoint feedback not only provided a salient cue for motor performance, but also signaled a strong causal relationship association between trials in which the cursor hit the target and the participant being awarded points. These signals would likely increase the participants' confidence that the outcomes reflect their motor performance, increasing their sense of agency and, thus, produce a stronger risk bias.

In addition to an overall sense of agency, there is another way in which reach feedback might influence choice behavior. The presence of reach feedback results in salient, "near miss" trials. These have been shown, at least under some conditions, to produce similar hemodynamic responses as are observed with rewarded trials (Clark et al., 2009). Treating these near miss outcomes as rewarding, even if only slightly, would result in a stronger risk bias when reach feedback was present in experiment 1, but not in experiment 2.

Mechanistic Considerations for the Modulation of Reinforcement Learning by Execution Errors

As noted in the Introduction, distinguishing between action execution and action selection errors is important to optimize choice behavior. Knocking over a cup of coffee should not make us dislike coffee, even though we failed to obtain an expected reward. Current models of decision making tend to be based on tasks in which execution errors are absent; yet these systems evolved in organisms in which outcomes almost always reflected the interaction of processes involved in selection and execution. We can envision two ways in which an execution error might gate value updating. The negative reward prediction error signals associated with unsuccessful outcomes might be attenuated. Or, the operation by which these signals modify value representations might be disrupted.

The SPE hypothesis was motivated, in part, by consideration of recently described projections between the cerebellum and basal ganglia (Hoshi et al., 2005; Bostan et al., 2010; Chen et al., 2014) and association areas of the cerebral cortex implicated in value representation (O’Doherty, 2004; Choi et al., 2012). We hypothesized that execution error signals, which evolved to keep the sensorimotor system calibrated, may have come to be exploited by the reinforcement learning system. However, the results from the current experiments provide strong evidence against this simple, bottom-up account of how a decision making system might distinguish between action execution and action selection errors.

Instead, the current results suggest that this gating process is driven by explicit knowledge about the source of errors, information that is dependent on a sense of agency. This contextual knowledge could have a direct influence on how reward prediction errors are computed or used to update value representations. The recruitment of working memory (Collins et al., 2017) and explicit knowledge about task contingencies (Li et al., 2011) have been shown to affect hemodynamic signatures of reward prediction errors in ventral striatum and ventromedial prefrontal cortex. In a similar fashion, top-down knowledge about the success or failure of action execution could provide a similar modulatory signal, either to a system generating reward prediction errors or using this information to update value representations. By using responses that offer the possibility of execution errors, it should be possible to use fMRI to identify neural loci that are sensitive to the intersection of action execution and action selection.

Chapter 2

Implicit adaptation is modulated by the relevance of feedback

Abstract

The motor system adapts to changes in the body and the environment by learning from sensory prediction errors, the difference between predicted and actual visual feedback. This process is highly automatic and implicit, with the response to the visual feedback occurring even when the resultant change from the sensory prediction error is detrimental to the task goal. In the real world, this visual feedback signal competes with other motion signals, only some of which may be relevant for the current goal. An open question is whether the insensitivity of adaptation to task goals holds when there are multiple sources of feedback. We address this question in the present study by simultaneously presenting multiple cursors in a center-out reaching task and varying the relevance of the cursors. Participants were instructed to hit a target with a specified (task-relevant) cursor, while ignoring the other cursors. If adaptation is insensitive to the relevance of the visual feedback signals, performance should be unaffected by the instructions. Alternatively, if adaptation is sensitive to task relevance, we would expect performance to be determined by the error associated with the task-relevant cursor. Neither hypothesis was supported by the results. In the context of multiple cursors, adaptation was dominated by the feedback associated with the task-relevant cursor. However, the amount of adaptation in the multi-cursor context was about half that observed in a single cursor condition; thus, the distractor feedback signals had an attenuating affect. These results highlight a novel role for task-relevance in implicit adaptation.

Introduction

The ability to produce accurate movements despite ongoing changes to one's body and environment requires continually using feedback to keep the sensorimotor system properly calibrated. This recalibration process is thought to be driven by sensory prediction error (SPE), the difference between the predicted and actual sensory feedback (Wolpert et al., 1995; Mazzoni and Krakauer, 2006; Kording et al., 2007; Burge et al., 2008; Chaisanguanthum et al., 2014). In this paper, we examine what happens when the sensory feedback is complex and ambiguous.

When performing goal-oriented movements in the real world, the visual field is cluttered, possibly obscuring the feedback of the movement (Körding and Wolpert, 2004; Burge et al., 2008; Wei, 2010) or even the target itself (Tipper et al., 1992, 1998; Howard and Tipper, 1997; Meegan and Tipper, 1998). Furthermore, the motion of other visual objects may be sources of distraction or interference. How does the motor system determine which signal is relevant for evaluating the consequences of an action, and how is this process influenced by the presence of competing visual signals?

Kasuga et al (2013) studied these questions using a center-out reaching task in which the participants could not see their moving arm, but had to rely on feedback provided by a moving cursor. On most trials, a single cursor reflecting the participants true hand position was presented. Interleaved with these were perturbation trials that rotated the cursor's trajectory by a random amount. On other perturbation trials, there were two or even three cursors, each following a different trajectory. For example, one cursor might correspond to the true hand position with the other cursor(s) rotated by varying amounts; or all of the cursors might be rotated from the true hand position. Given that the number of cursors and rotations of the cursors was randomized across trials, implicit adaptation was measured by calculating the trial-by-trial change in hand angle. The results showed that the size of the trial-by-trial change could be modeled by taking the average predicted response to each of the individual cursors, albeit with a global attenuation in comparison to the single cursor condition. Thus, the response to two cursors, one at 0° (veridical feedback) and one rotated by 45° was similar to when there were two rotated cursors, one at 15° and one at 30° . The fact that there was adaptation even in the former case is especially surprising given that one cursor provided veridical feedback. The adaptation system did not appear to be preferentially sensitive to veridical feedback.

One issue of note in the Kasuga study is that, from the participants' perspective, all of the cursors were equally important and relevant to the task. Under such conditions, it may be appropriate to produce a composite error signal. However, in a natural environment, there is likely to be one relevant source of feedback amongst irrelevant and potentially distracting sources of information. An important question is whether sensorimotor adaptation is sensitive to the relevance of available feedback. Reichenbach et al. (2014) provided a compelling demonstration that the motor system was indeed sensitive to the relevancy of visual signals. Participants performed reaching movements in which the feedback display included one cursor linked to the true hand position as well as up to 4 distractor cursors that moved with a similar but predetermined, and thus non-contingent velocity profile. At some point during the movement, one of the cursors made an abrupt lateral shift. Rapid, online corrections to the perturbation were much stronger when the perturbed cursor was the one linked to the hand position, compared to when the perturbed cursor was one of the distractors. Similar effects of task relevance have been observed in force-field adaptation studies (Heald et al., 2018), suggesting that implicit motor processes required for both on-line corrections and adaptation are sensitive to the task-relevance of different feedback signals.

In contrast, other lines of research have highlighted how sensorimotor adaptation is seemingly impervious to feedback regarding task goals and outcomes. Consider the aiming landmark task, first introduced by Mazzoni and Krakauer, (2006). After being briefly exposed to a 45° visuomotor rotation, the participants were instructed to aim to a landmark positioned 45° in the opposite direction from the target. By implementing this strategy, the participants were essentially perfect after one trial, producing movements in which the rotated cursor hit the target. Nonetheless, over the next 100 trials or so, performance deteriorated, with the hand angle increasing even further away from the target (see also Taylor and Ivry, 2011). This paradoxical result arises because the adaptation system, impervious to the strategy, recalibrates the sensorimotor mapping to reduce the SPE, here defined as the difference between where the movement was directed (towards the landmark) and where the cursor appeared (at the target). Similarly, participants implicitly adapt to the movement of a cursor that follows an invariant spatial trajectory displaced from the target, even when they are fully aware of the manipulation and told to ignore it (Morehead et al., 2017; Kim et al., 2018; Parvin et al., 2018).

Experiments such as these have led to the view that implicit adaptation is solely dependent on SPE, and impervious to feedback concerning the task outcome (but see Kim et al., 2019). The results from the multiple cursor study of Kasuga et al. (2013) would also be consistent with this hypothesis. However, as noted above, the cursors were, in a sense, all task-relevant. Here we employ a multiple cursor task similar to Kasuga *et al.*, but with two key changes. First, rather than randomize the perturbation from trial-to-trial, we employed a fixed rotation throughout the training period and assessed adaptation in a subsequent block in which all feedback was withheld. Second, and most importantly, we varied the cursor configurations and instructions as a way to manipulate the task relevance of the different feedback signals. In this way, we sought to determine whether implicit adaptation is sensitive to the relevance of the feedback.

Methods

Participants

Undergraduate students ($n = 64$, 41 female, age = 20 ± 2 years) were recruited from the University of California, Berkeley community and financially compensated for their participation in the experiment. All participants were right handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). The research protocol was approved by the UCB institutional review board.

Experimental Apparatus

The participant was seated in front of a horizontally oriented computer monitor that was supported by a table frame. All hand movements were tracked on a digitizing tablet (53.2 cm x 30 cm, ASUS), positioned 27 cm below the monitor. The participant held a modified air hockey ‘paddle’ embedded with a digitizing stylus to make center-out reaching movements over the tablet surface in response to visual stimuli displayed on the monitor. The participant’s hand was occluded by the table/monitor, and the room was minimally lit to further preclude visual feedback of the arm. The latency between the movement of the digitizing stylus and the updating of the cursor position on the monitor was 33 ms. The experimental code, controlling the visual display and acquisition of kinematic information was written in MATLAB, using the Psychophysics toolbox extensions (Pelli, 1997).

Overview of the reaching task

Participants performed 8 cm reaches to targets located around a central starting location. The start location was indicated by a 6 mm white annulus, and the target was a 6 mm blue circle. The visual displays also included feedback cursors (3.5 mm white circles) that, depending on the condition, either corresponded to the participant’s hand position or were rotated at a fixed angle from the hand position.

In all conditions, participants were instructed to produce rapid movements such that the task-relevant designated cursor would ‘shoot’ through the target. Movement onset was arbitrarily

defined as the time at which movement amplitude reached 1 cm from the center of the start position. Movement time (MT) was defined as the duration from this point until the hand reached a radial distance of 8 cm, the target distance. Auditory feedback concerning MT was used to encourage participants to make relatively fast movements. For reaches shorter than 100 ms or longer than 300 ms, the messages ‘too fast’ or ‘too slow’ were played over the computer speaker. A neutral ‘knock’ sound was given if MT fell within the desired range. Across all trials, the median reaction time (RT) and MT were 462 ms and 172 ms, respectively. The median total trial time (TTT), defined as the time from the start of one trial to the start of the next, was 3714 ms. One way ANOVAs revealed no differences between groups for RT ($F(3, 44) = 0.448, p = 0.720$), MT ($F(3, 44) = 1.336, p = 0.275$), or TTT ($F(3, 44) = 0.245, p = 0.865$).

On trials with visual feedback, the cursor or cursors were visible until the movement amplitude reached 8 cm, whereupon the end point position was frozen for an additional 1 s. By freezing the cursors, the participant received additional endpoint feedback of performance accuracy. At the end of the feedback period, the cursors were turned off and the participant moved their hand back to the start position. To help the participant find the start position, veridical feedback was provided when their hand was within 1 cm of the start position. Once in the start position, the feedback cursor was turned off and the annulus filled, indicating that the participant should prepare for the next trial. The next target appeared once the participant remained within the starting position for 500 ms.

Experiment 1

Experiments 1a and 1b ($n = 48, 12$ per group) employed a similar design in which the participant completed a series of five blocks. The No Feedback Baseline block was composed of 24 reaches without visual feedback, one to each of 24 targets evenly spaced at 15° intervals (0° to 345° , with 0° corresponding to a rightward movement). This block was included to familiarize the participants with the experimental apparatus and with making movements in the desired time. The next block, Feedback Baseline, was composed of 10 cycles of reaches, with each cycle composed of one reach to each of the 24 target locations (240 trials). Veridical online feedback was provided by a feedback cursor aligned with the participants’ hand. Next was the Training block in which the specific experimental manipulations of the cursor feedback were introduced (detailed below). Targets were limited to three locations ($30^\circ, 150^\circ, 270^\circ$) with 80 cycles of 3-target sets (Training, 240 total trials). The 120° spacing was chosen to minimize generalization/interference of adaptation effects between the three training locations (Krakauer et al., 2000; Day et al., 2016). The Aftereffect block had one cycle of 24 trials with participants reaching to each target without visual feedback, similar to No Feedback Baseline. At the start of this block, the participant was explicitly instructed to reach directly to the target. The Washout block had the same structure but with veridical visual feedback (3 cycles, or 72 trials). The Aftereffect and Washout blocks provided the critical data to test for aftereffects, indicative of implicit adaptation and generalization. In all blocks, the order of the target location was randomized within a cycle.

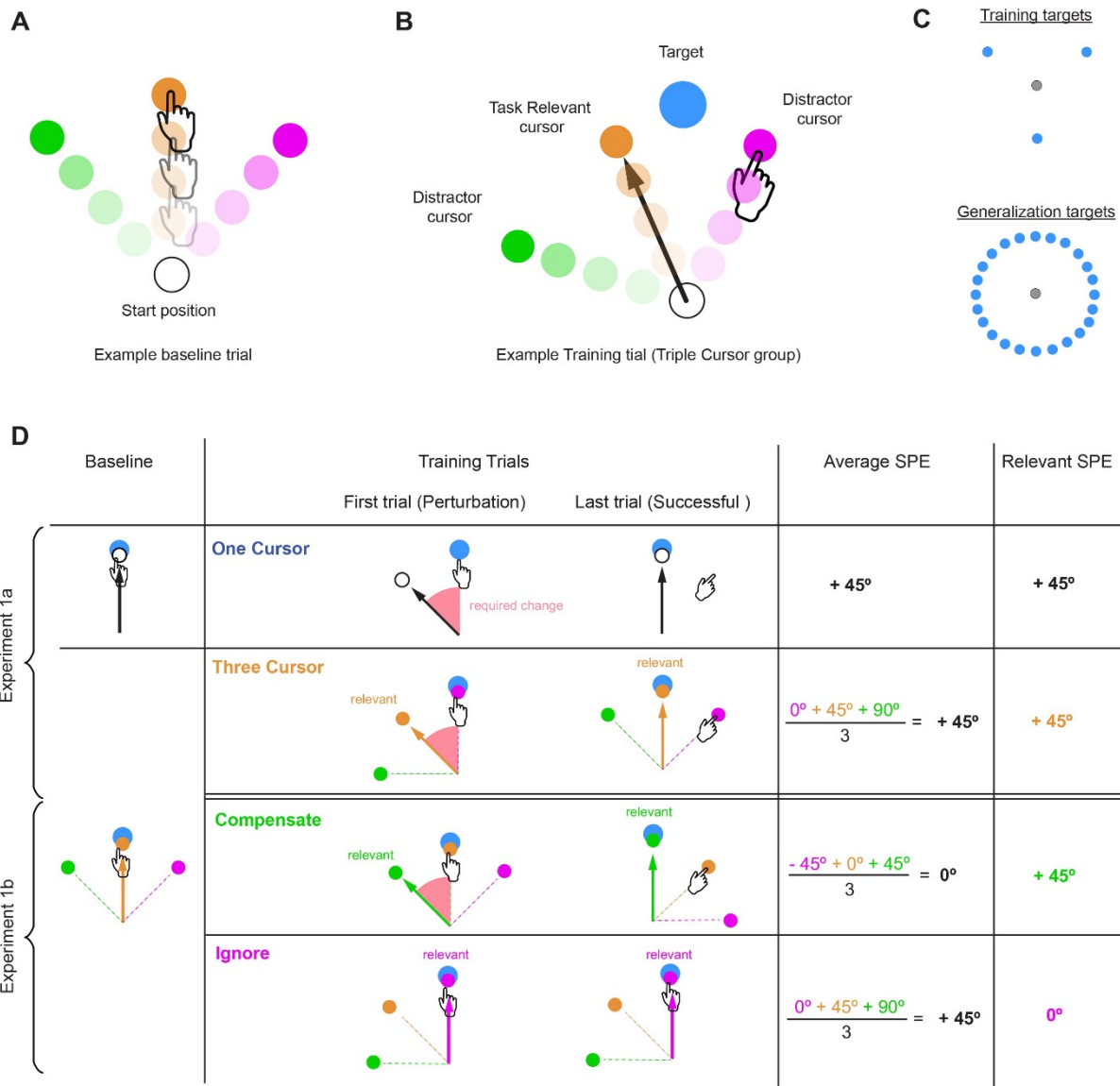


Figure 2.1 Cursor feedback configurations for Experiment 1. A) Example baseline trial for the Three-Cursor group. The middle cursor follows the veridical hand position with two additional cursors rotated either $\pm 45^\circ$ on either side. The cursor color arrangement is counterbalanced across subjects. Participants are told to reach directly to the target with the middle cursor. B) Example training trial for the Three-Cursor group. All the cursors are rotated by 45° so that the middle cursor no longer corresponds to the true hand position. Participants are told to hit the target with the middle cursor and ignore the other two. C) Target locations for Experiment 1. For training trials, targets appeared in three locations (30° , 150° , 270°). In all other blocks, targets appeared in 24 generalized locations (from 0° to 345° in 15° intervals). D) Experimental conditions for Experiment 1. Experiment 1a compares learning from one cursor versus three cursors, keeping average and relevant SPE the same. Experiment 1b employs two additional multiple cursor conditions to understand how the distractor cursors affect adaptation. The Compensate group did not have a cursor rotation, but the relevance of the cursors changed. One of the distractor cursors was assigned to be relevant (the middle cursor is now irrelevant and ignored), changing the average SPE but keeping the relevant SPE the same. The Ignore group experienced a cursor rotation and a relevance change, keeping the average SPE the same but changing the relevant SPE. These participants were told to hit the target with the cursor that now followed their veridical hand position.

Experiment 1a

Experiment 1a was designed to examine the influence of distractor cursors on performance during a visuomotor rotation task. We compared performance between training conditions in which the display contained a single feedback cursor rotated 45° from the true hand position or when the display also contained two additional cursors, positioned $\pm 45^\circ$ relative to the single cursor (Fig 1D).

One Cursor group (n=12): A single feedback cursor was visible during the blocks with visual feedback. In the Feedback Baseline and Washout blocks, the cursor provided veridical feedback. At the start of the Training block, the participant was informed that the feedback cursor would no longer be veridical, but would now be displaced by 45° relative to their hand position (counterbalanced clockwise or counterclockwise across participants). They were instructed that the task goal was to compensate for this rotation such that the rotated cursor would hit the target. The experimenter explained the effect of the rotation on the cursor and the new task by illustrating it on a whiteboard. Although it could be inferred from the instructions that they could re-aim 45° away from the target to achieve the goal, we did not explicitly instruct them to use such a strategy. By making the rotation explicit, we believed there would be less ambiguity in the Aftereffect and Washout blocks, in which we assess implicit adaptation by instructing participants to reach directly with their hand. Furthermore, since participants were informed about the rotation of the cursors in the Three Cursor group (below), this made the number of cursors the only difference between the two groups.

Three Cursor group (n=12): Three feedback cursors were visible during each of the blocks with visual feedback, with the cursors separated by 45° . Each cursor had a unique color: green, orange, and purple (RGB values (/255) [7 210 0], [231 145 53], [234 0 238] respectively). All colors were approximately matched on luminance based on a 'Hue Chrome Luminance' color scheme, and the assignment of color to cursor was counterbalanced across participants. In the Feedback Baseline and Washout blocks, the participant was informed that the middle cursor would correspond to the true hand position and instructed to hit the target with that cursor, specified in terms of the cursor color, idiosyncratic for each participant. This cursor was flanked by the two distractor cursors, resulting in three cursors moving at -45° , 0° , 45° , relative to hand position (Figure 1). The participant was instructed to ignore the other two cursors. Thus, if the color assignment for the -45° , 0° , 45° cursors was green, orange, and purple respectively, then the participant was to hit the target with the orange cursor and ignore the green and purple cursors.

During the Training block, all three cursors were rotated by 45° , such that the cursors now appeared at 0° , 45° , 90° (or 0° , -45° , -90° , counterbalanced across participants) relative to the true hand position. The participant was informed of the manipulation and instructed to hit the target with the middle cursor. Since the relative color assignment of the cursors remained the same, the instructions did not change. Using the color mapping example from above with a counterclockwise rotation, the participant's goal was still to hit the target with the orange cursor (now rotated 45° from true hand position), while ignoring the green and purple cursors. With this arrangement, the purple cursor now ended up corresponding to the true hand position (0°) and the green cursor was rotated by 90° , relative to the hand. As such, if each cursor were to contribute equally to form a composite SPE (Kasuga et al., 2013), the net SPE in the Three Cursor condition is identical to that in the One Cursor condition.

Experiment 1b

As reported below, the inclusion of the two task-irrelevant distractors attenuated adaptation in the Three Cursor group, relative to the single-cursor group. Experiment 1b was designed to test two hypotheses that could account for this attenuation. The first hypothesis, “Error Averaging”, posits that adaptation is equally driven by SPE signals generated from all three cursors, but that their weightings add up to less than 1. Thus, the total amount of adaptation resulting from a 0°, 45°, and 90° would be less than from just one 45° cursor. The second, “Non-Specific”, hypothesis is that the presence of distractors dilutes the effects of adaptation in a general manner, and as such, the attenuation effect is not dependent on the particular path of the distractor cursors. To evaluate these hypotheses, we compared two three-cursor variants in Experiment 1b, using the same trial structure as in Experiment 1a.

In the Compensate group ($n = 12$), the visual feedback was not rotated during the Training block. Instead, the participants were instructed to hit the target with the side (45°) cursor. For example, if the participant was in the clockwise group (counterbalanced across participants) and had the color mapping as shown in Figure 1D, they were instructed to hit the target with the green cursor. “Compensate” refers to the fact that, while the three cursors were not rotated relative to baseline, the instructions required participants to compensate for the angular offset of the task-relevant cursor. Note that as a result of this change in instructions, the angular offset of task-relevant cursor from the hand position (by 45°) is similar to the Three Cursor condition in Experiment 1a.

In the Ignore Rotation group ($n = 12$), the three cursors were rotated by 45° in the Training block. However, unlike Experiment 1a, the task goal was changed for this block, with the participant instructed to hit the target with the outer cursor that was in the opposite direction of the rotation (e.g., for a counterclockwise rotation, the task-relevant cursor now became the cursor that was clockwise to the center cursor). As shown in Fig. 2, the net effect of the rotation and change in instructions results in the task-relevant cursor corresponding to the position of the hand. “Ignore” here refers to the fact that participants can ignore the 45° rotation applied to the three cursors since the task-relevant cursor ends up being veridical with respect to the participant’s hand.

In summary, the groups used in Experiment 1a and 1b allow us to compare, relative to the single-cursor condition, three multiple cursor groups that vary in terms of their average SPE and task-relevant SPE (Figure 1D). Furthermore, with the exception of the Ignore condition, all groups were required to make a 45° change in reaching angle in the Training block to compensate for the perturbation, making reaching behavior very similar across these groups.

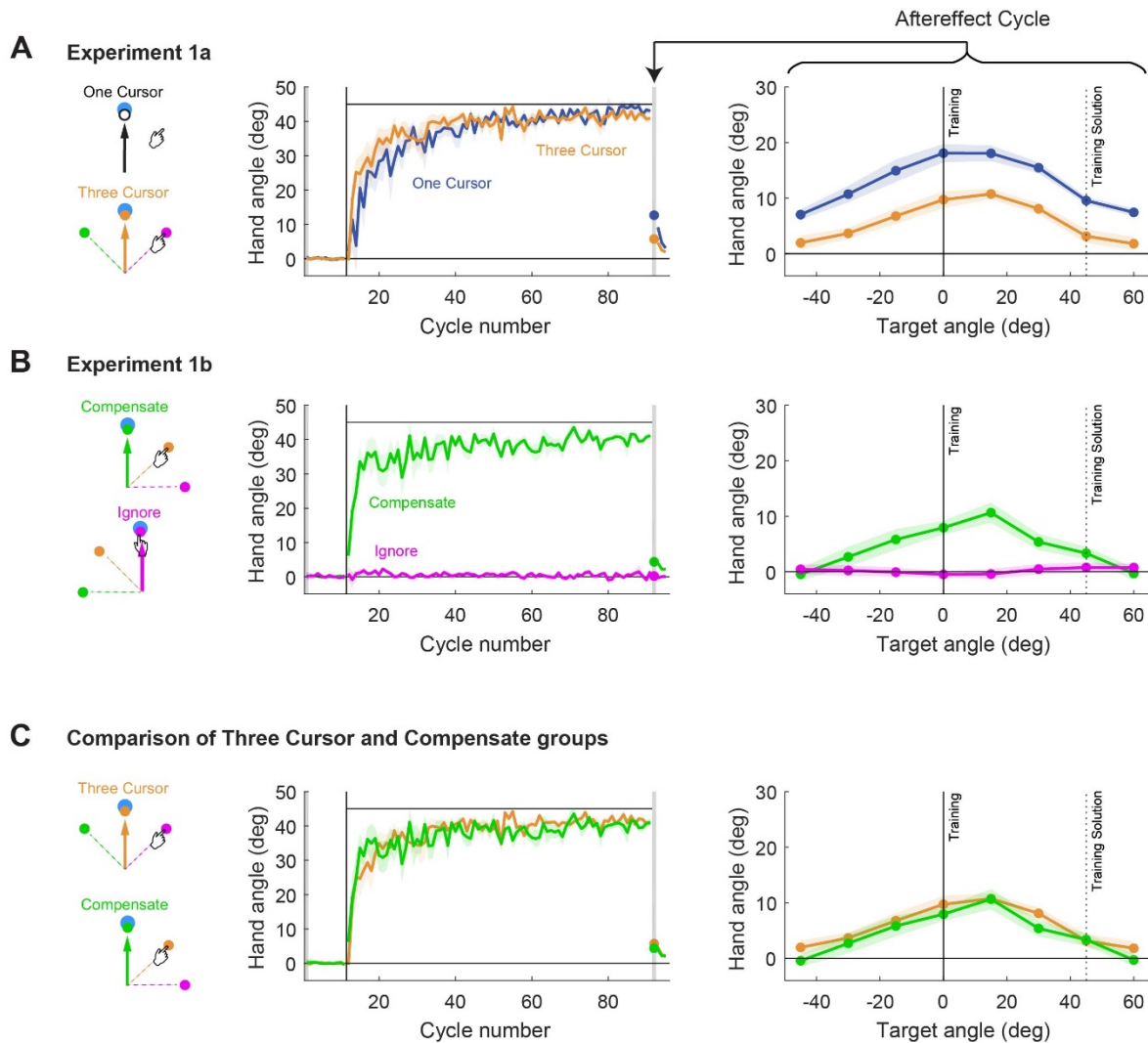


Figure 2.2 Experiment 1 Results A) Left, Comparing reaches across the experiment between the One Cursor (blue) and Three Cursor (orange) conditions. Both groups learn and compensate for the rotation at the same rate during training. Right, After the training block, participants were instructed to reach directly to the generalization targets; no feedback was provided. The centers of the generalization curves' peaks are not significantly different, but the magnitudes are. B) Left, Hand reaches for the Compensate and Ignore group in Experiment 1b. Right, Significant aftereffects only seen for the Compensate group. C) Directly comparing behavior between the Three Cursor and Compensate group. No significant differences in either the training (left) or aftereffect (right) periods. Thick lines are group means with the shaded regions indicating +/- SEM.

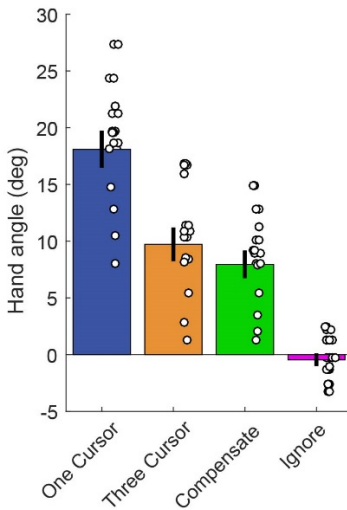


Figure 2.3 Aftereffects of Experiment 1 Three Cursor and Compensate groups have similar levels of adaptation that are both significantly less than the One Cursor group and significantly greater than the Ignore group. Data are group mean +/- SEM with dots to indicate individual means

Results

Experiment 1a

In Experiment 1, we examined the impact of task-irrelevant cursors on implicit adaptation. We first compared adaptation to displays consisting of either a single cursor (One Cursor group) or three cursors, separated by 45° (Three Cursor group, Fig 2). In both groups, participants were informed that, during the training block, the task-relevant cursor (single or middle) was rotated by 45° relative to their hand position, and that their task was to hit the target with this cursor. In the Three Cursor group, participants were also told that one of the distractor cursors would coincide with their veridical hand position but that they should ignore it and focus on the task-relevant cursor.

Performance of the two groups during the Training block was compared to assess effects of the distractor cursors on overall learning. Both groups appeared to compensate for the perturbation at a similar rate and extent. There were no significant differences in early learning (cycles 3-7, One Cursor mean hand angle = 18.00° [9.90°, 26.10°], Three Cursor mean = 26.67° [17.23°, 36.12°], [t(22) = -1.535, p = 0.139, d = -0.626]), nor in late learning (last 10 cycles, One Cursor mean = 43.44° [41.27°, 45.62°], Three Cursor mean = 41.55° [40.14°, 42.96°], [t(22) = 1.608, p = 0.122, d = 0.656]). Previous studies have shown that implicit adaptation is typically limited to 10°-25° of learning (Bond and Taylor, 2015; Morehead et al., 2017; Kim et al., 2018). Given that the change in hand angle is much larger than this range and that the participants were explicitly informed of the manipulation, we assume there is a strategic, aiming contribution to performance here. As such, the results indicate that the distractor cursors did not have an appreciable influence on the participants' ability to adopt an aiming strategy to complement adaptation.

To assess implicit adaptation, we included a block of trials after training in which the cursor was no longer presented (no visual feedback), and participants were instructed to reach directly towards the target. Both groups exhibited aftereffects at the trained target location. However, the magnitude of adaptation differed for the two groups: The One Cursor group had a significantly greater aftereffect than the Three Cursor group (One Cursor group = 18.10° [14.50°, 21.69°], Three Cursor group = 9.72° [6.48°, 12.96°], [t(22) = 3.808, p 9.622e-4, d = 1.555]).

There are at least two reasons why the aftereffect would be larger in the One Cursor group. First, the difference could reflect that adaptation is attenuated by the inclusion of task-irrelevant distractors. Alternatively, there could be a group difference in the use of an aiming strategy. Assuming that the generalization function for adaptation is centered on the aiming location (Day et al., 2016), differences in strategy use could cause differences in measured adaptation at the training location on aftereffect trials.

To evaluate these two hypotheses, we assessed generalization during the aftereffect block by measuring adaptation across a set of probe targets that spanned the work space in 15° increments (Figure 1C). The attenuation hypothesis predicts that the functions would be aligned but with a lower peak for the Three Cursor group; the aiming hypothesis predicts that the functions would be similar in amplitude but misaligned. The results were consistent with the attenuation hypothesis. While the generalization functions for both groups were shifted towards the presumed aiming direction of aiming, the peak of the generalization function was similar for the two groups. Based on parameters obtained when fitting a Gaussian curve to the group data, the peak of the generalization function was 7.7° [4.4, 10.9] and 9.0° [5.1, 12.8] for the One Cursor and Three Cursor group respectively [mean, bootstrapped 95% CI]. In contrast, the heights of the peaks were different for the two groups (One Cursor: 18.8° [16.7, 20.8]; Three Cursor: 11.0° [9.3 12.2]). These findings suggest that the presence of the additional cursors attenuated the degree of implicit adaptation.

Error Averaging vs Relevant error models of adaptation

We next asked how the inclusion of the distractor cursors in the Three Cursor group influenced adaptation. Specifically, we wanted to determine whether the direction of the distractor cursors mattered. We formulated two possible models to account for the attenuation.

The Error Averaging model, inspired by Kasuga and colleagues (Kasuga et al., 2013), proposes that the error from each cursor is processed simultaneously and contributes towards learning (Equation 1). By this model, the attenuation effect for the Three Cursor group is reflected in a reduction in the learning term, B_t , relative to what it would be in the single cursor case. Kasuga and colleagues observed a reduction of 0.57 for B_t in their three cursor conditions relative to the single cursor condition. This value is consistent with our observed attenuation of 0.55 for three cursors in Experiment 1a (Three Cursor aftereffect divided by the One Cursor aftereffect).

$$x_{n+1} = A * x_n + B_t * \frac{e_{relevant} + e_{distractor\ 1} + e_{distractor\ 2}}{3} \quad \text{Equation 1}$$

An alternative model, the Relevant Error model, proposes that implicit adaptation learns selectively from the relevant error, while the distractor cursors attenuate adaptation in a non-specific fashion. Thus, the directions of the distractor cursors have no bearing on the direction or magnitude of the aftereffect. The attenuation due to the presence of the two distractor cursors would also be manifest in a reduced B_t term, just as in the Error Averaging model (Equation 2).

$$x_{n+1} = A * x_n + B_t * e_{relevant} \quad \text{Equation 2}$$

To compare these two models, we tested two additional groups in Experiment 1b.

Experiment 1b

The difference between the two models is in their treatment of the distractor cursors. In the Error Averaging model, feedback information from each cursor is equally weighted to form a composite error signal, whereas in the Relevant Error model, only the feedback information from the task relevant cursor is used to define the error signal. Given that Error Averaging and Relevant Error models make identical predictions for the Three Cursor group, we devised two new three cursor variants that yield divergent predictions for the two models.

In the Compensate group (Figure 2), the mapping between hand position and cursor is not changed in the Training block; that is, the cursor that provided veridical feedback during the initial Feedback block continues to provide veridical feedback in the Training block. However, the instructions change, with the task goal now requiring the participant to hit the target with the cursor that is offset 45° from the hand (45° clockwise or counter clockwise, counterbalanced across participants). To achieve this, the participant must move in the opposite direction (e.g., clockwise if task goal is to hit target with counter clockwise cursor). While the required hand trajectory is the same as in the Three Cursor group, the set of errors is different. For the Compensate group, the sum is now 0° (-45° , 0° , 45° , relative to the hand direction). Thus, the Error Averaging model would predict no adaptation. In contrast, the Relevant Error model would predict the same amount of adaptation as observed with the Three Cursor group. Even though the errors from the distractor cursors are different between the Compensate and Three Cursor groups, both have a task relevant cursor that is offset by 45° from the hand direction.

Consistent with the Relevant Error prediction, participants exhibited a robust aftereffect with Gaussian shaped generalization (mean at training location = 7.95° [5.26° , 10.63°], $t(11) = 6.510$, $p = 4.368e-5$, $d = 1.879$). Furthermore, the Compensate group behaved similarly to the Three Cursor group during both the Training and Aftereffect blocks. There were no significant differences during the Training block in their early learning (mean and 95% CI, Three Cursor = 26.67° [17.22° , 36.11°], Compensate = 32.09° [25.70° , 38.48°], [$t(22) = -1.047$, $p = 0.306$, $d = -0.428$]), nor in their late learning (mean and 95% CI, Three Cursor = 41.55° [40.14° , 42.96°], Compensate = 40.37° [38.34° , 42.40°], [$t(22) = 1.053$, $p = 0.304$, $d = 0.430$]). There were also no significant differences in their aftereffects at the training locations (Three Cursor mean = 9.72° [6.48° , 12.96°], Compensate mean = 7.95° [5.26° , 10.63°], $t(22) = 0.925$, $p = 0.365$).

The Ignore group provided a second test of the models. Here, a rotation of all three cursors was introduced during the Training block, identical to that used for the Three Cursor group. However, the participants were instructed in this block to hit the target with the 0° cursor, the one that was now veridical with hand position. “Ignore” refers to the fact that the participant’s task was essentially to ignore the rotation by focusing on the (new) cursor that matched their hand position. The Error Averaging model predicts the same aftereffect as the Three Cursor group, since it is insensitive to the relevance of the error signals and the average error is again 45° (90°, 45°, 0°, relative to the hand direction). The Relevant Error model, on the other hand, predicts no aftereffect, since the hand direction and task-relevant cursor are aligned. Again, the results of the aftereffects conformed to the Relevant Error prediction. A t-test showed no significant aftereffect at the training location (mean = -0.45° [-1.66°, 0.75°], $t(11) = -0.833$, $p = 0.423$, $d = -0.240$).

The training period of the Ignore group lent itself to testing another prediction of the Error Averaging hypothesis. If a composite SPE was present during the training trials, we should observe a ‘drift’ away from the target, despite initial accurate performance (Mazzoni and Krakauer, 2006; Taylor and Ivry, 2011). A t-test against 0 produced a non-significant result (mean = 0.57° [-0.20°, 1.33°], $t(11) = 1.635$, $p = 0.130$, $d = 0.472$). We were worried, however, that this measure would not be sufficiently sensitive to capture what might be a transient effect (Taylor and Ivry, 2011). As a more sensitive alternative, we opted for a cluster analysis, assessing if there were any consecutive cycles with significant drift (see supplementary information). This approach identified a significant cluster of two consecutive cycles (training cycles 10 and 11) in which the mean hand angle was greater than 0° (mean = 1.95° [1.09°, 2.81°], $t(11) = 4.992$, $p = 4.076e-4$, $d = 1.441$). While this small cluster is in the expected direction, it is very small and of shorter duration than that observed in previous studies (e.g., a 15° drift that lasts for about 80-100 trials, see Taylor & Ivry [2011]). Thus, if there was any implicit adaptation in the ignore group, it was very limited.

Overall, the results rule out the Error Averaging model and are consistent with the Relevant Error model: Significant aftereffects were observed when the task relevant cursor was offset 45° from the hand position during the Training block, either because we imposed a perturbation or altered the instructions. Moreover, the results from the Ignore group, as well as the similarities between the Compensate and the Three Cursor group, suggest there is minimal, or no specific influence from the distractor cursors. Rather, the presence of the distractors appears to have a non-specific attenuation effect on adaptation to the task-relevant cursor.

Experiment 2

Although the results of our first experiments suggest that task relevance modulates adaptation, they are far from conclusive in this regard. Not only was there no imposed rotation for the Ignore group-- just a change in the task-relevant color in the Training block, but this group also did not have to aim away from the target (as in the Compensate group). To provide a more direct assessment of the contribution of task-irrelevant information, we conducted a second experiment using a design in which there were two targets, positioned approximately 90° apart, and two associated cursors, one rotated 45° in the clockwise direction from the hand direction and the other rotated 45° in the counter-clockwise direction (Figure 4A). One target/cursor was designated task relevant and the other was designated a distractor (i.e., task irrelevant). Regardless of which was

task relevant, the movement required to hit the target was directed around the midpoint of the two targets, resulting in each cursor landing nears its associated target. We measured the aftereffects around each target location to determine the degree of adaptation. We hypothesized that the task relevant target may form the locus of generalization for implicit adaptation. Therefore, whether there is also an aftereffect around the distractor target was of primary interest.

To verify that participants were following the instructions, we jittered the exact position of the targets (see Methods) and calculated the trial-by-trial hand angle relative to each target (Figure 4D). Using these time series, we then performed a multiple regression using the positions of the relevant and distractor targets on each trial to predict the hand angle. This analysis produced a beta weight for each target, quantifying how much the participant's behavior reflected the tracking of each target (Figure 4E). We saw that greater weight was given to the task relevant target in 15 of the 16 participants. The other participant appeared to not follow directions (beta weights were -0.14 and 0.09 for the relevant and distractor targets), and this person's data were excluded from the remaining analyses.

The mean beta weight for the task relevant target was 0.76 [0.67, 0.84] and for the distractor target was 0.20 [0.09, 0.32]. These values were significantly different from one another ($t(28) = 8.149$, $p = 7.16e-9$, $d = 2.975$). Interestingly, the beta weight for the task distractor target was significantly greater than zero ($t(14) = 3.675$, $p = 0.002$, $d = 0.949$). Thus, while the participants followed the instruction to track the relevant target, the results indicate that the participants were not able to completely ignore the distractor target. One possibility is that the distractor target may have served as an additional visual reference for aiming.

To assess adaptation, participants made reaching movements without feedback to an array of targets, spanning the workspace that encompassed the two positions of the targets during the training block. As in Experiment 1, the participants were instructed to reach directly towards each target. To analyze these data, we collapsed across the two groups (clockwise or counterclockwise rotation of the task relevant cursor), displaying the data as though all participants were instructed to hit the clockwise target and ignore the counterclockwise target (Figure 4B). A significant aftereffect in the direction consistent with the rotation was observed around the task-relevant target location (mean 10.87° [6.48° , 15.27°], $t(14) = 5.304$, $p = 1.114e-4$, $d = 1.370$). Interestingly, there was also a significant aftereffect at the distractor target location (mean -4.37° [-8.27° , -0.47°], $t(14) = -2.406$, $p = 0.031$, $d = -0.621$). The negative aftereffect associated with the distractor target was consistent with the distractor cursor having the opposite rotation to the relevant cursor. A direct comparison of the two effects showed that the unsigned aftereffect was larger at the relevant target location ($t(28) = 2.373$, $p = 0.025$).

The fact that we observed a small aftereffect around the distractor target location would seem at odds with the results of Experiment 1 where the effect of the distractor cursors was not dependent on their direction (e.g., non-specific attenuation). However, as shown in the beta weight analysis, the participants in Experiment 2 did not completely ignore the distractor target. We looked at the correlation between beta weights and magnitude of the aftereffect for both the relevant and distractor locations to look at the relationship between tracking and adaptation. To capture how much a participant weighted the relevant target over the distractor, we normalized the beta weights (beta weight for relevant target / sum of both beta weights) in these correlations. For the relevant location, the correlation was significant ($r = 0.67$ $p = 0.007$), meaning that those who were most successful in tracking the relevant target had the largest aftereffect around that target's associated

location. We performed the same analysis for the distractor target to see if the same relationship held true. Since the distractor cursor had the opposite rotation, the predicted correlation would be negative. This analysis revealed a similar pattern, but the correlation was not significant ($r = -0.30$, $p = 0.274$). We note that the range of values is much narrower for the distractor location compared to the relevant location.

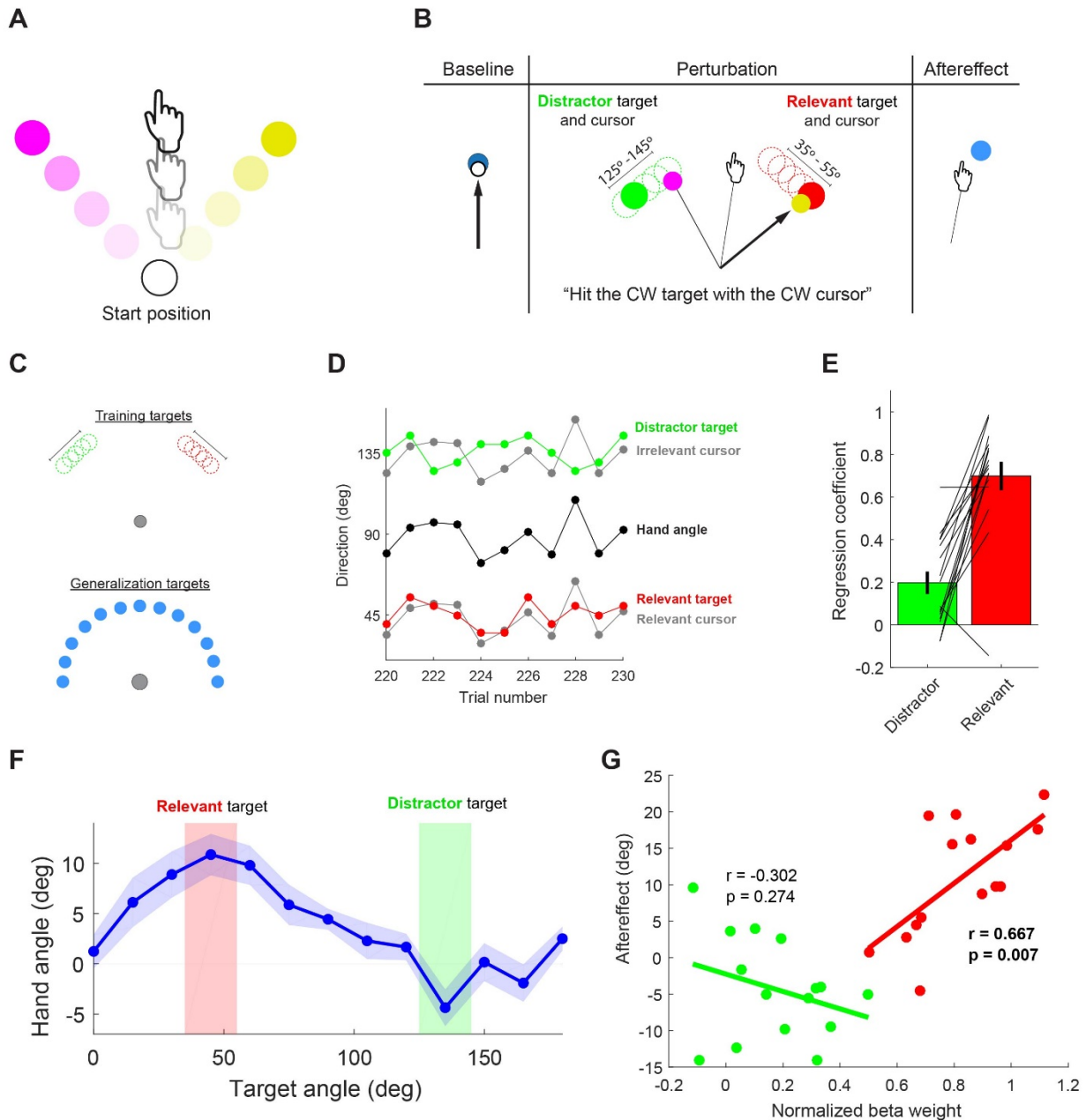


Figure 2.4 Experiment 2 Results. A) Cursor feedback configuration for training trials. Two cursors appear during the reach rotated $\pm 45^\circ$ to veridical hand position. B) Experimental task. Baseline and aftereffect trials had one cursor feedback reaches to generalization targets. During training, one target/cursor pair assigned task relevance that participants were instructed to solely focus on. Targets jittered to later assess how well participants track the relevant target. C) Target locations. Reaches limited to one half of the workspace. Top, training targets appear around $\pm 45^\circ$ from the center of the given workspace. Location of each target independently jittered by one of 5 values: -10° , -5° , 0° , 5° , 10° . Bottom, 13 generalization targets spaced 15° apart. D) Trial by trial tracking behavior for distractor (green) and relevant (red) target/cursor pairs. E) Beta weight for relevant target (red) significantly greater than the non-zero beta weight for the distractor target (green). Data are group mean \pm SEM with lines representing individual performance. F) Generalized aftereffects. Significant in the relevant location (red), as well as in the distractor direction (green) but to a smaller degree. G) Correlation between beta weights and aftereffect for relevant and distractor targets. Significant correlation for the relevant target (red) shows that participants who were better at tracking also had larger aftereffects. Non-significant correlation for distractor target (green). Note that in Panels D and F, the data are transformed to graphically depict the relevant target at 45° for all participants.

Discussion

In this study, we asked how implicit adaptation, an important process for maintaining calibration of the sensorimotor system, is affected by the presence of multiple visual signals. Through our use of task instructions, we varied the information value of the signals, designating one cursor as task relevant and the others as task irrelevant. We found that adaptation was sensitive to the rotation of the task relevant cursor. Moreover, as shown in Experiment 2, the degree to which participants tracked the target with the relevant cursor predicted the size of their aftereffect, pointing to a strong relationship between the task relevance assigned to the cursor and the amount of adaptation. Interestingly, implicit adaptation was attenuated by the presence of distracting feedback, but this effect was non-specific: The presence of the distractor cursors reduced the magnitude of adaptation, but not the direction of their movement. These findings highlight a novel role of task relevance for implicit adaptation.

Adaptation is sensitive to task relevance

By presenting multiple cursors and manipulating their relevance, we were able to make sense of two seemingly contradictory conclusions about the motor system. The results from several studies suggest the motor system is sensitive to the relevance of feedback (Reichenbach et al., 2014; Heald et al., 2018). In contrast, the results from other studies have shown that implicit adaptation is insensitive to task goals. For example, when only one cursor is presented, implicit adaptation will learn from the SPE, regardless of whether participants are explicitly told to ignore the visual feedback, or even when the response to that cursor is detrimental to performance (Mazzoni and Krakauer, 2006; Taylor et al., 2010; Taylor and Ivry, 2011; Morehead et al., 2017). The results from the current study suggest a hybrid position: When more than one source of feedback is present, the input to adaptation can be restricted to the most relevant source of feedback. This

selectivity constraint has been observed in studies of other implicit motor functions, such as the finding that online corrections are faster in response to perturbations of a task-relevant cursor (Reichenbach et al, 2014) or that separate force fields can be learned depending on what part of a virtual tool is deemed relevant (Heald et al, 2018).

Using a one-way mirror and a light to manipulate vision of the hand, Wong et al (2019) showed that when participants simultaneously can see their hand and a rotated cursor, adaptation (to the cursor) is abolished. In our conditions involving three cursors, one cursor always corresponded to the veridical hand position, and the participants were aware of this relationship. Nonetheless, the Three Cursor and Compensate groups still exhibited unambiguous implicit adaptation. Moreover, while the aftereffect in these groups was attenuated relative to the One Cursor group, the magnitude of adaptation was similar to that observed in Experiment 2 and in Kasuga et al. (2013), conditions in which there was no cursor was aligned with hand position. Thus, it appears that the presence of a veridical feedback signal had no additional effect on attenuation, a result that is at odds with the findings of Wong et al. (2019). We suggest that the system modulating the input to adaptation is sensitive to the overall form of the feedback. Seeing an actual hand may be more compelling than cursor feedback, giving it precedence over the cursor feedback, even if this is at odds with the task goal.

Selectivity of feedback is imperfect

Although adaptation was sensitive to the relevance of the feedback, the overall attenuation of learning demonstrated that the selectivity was imperfect. The presence of multiple cursors had a similar attenuating effect in the present study as in Kasuga and colleagues (2013). Specifically, adaptation was attenuated by about 45% when there were three cursors relative to a standard single cursor in both studies. This similarity is striking given that Kasuga used unpredictable rotations, interleaved the single and multi-cursor conditions, provided no instructions concerning relevance, and measured learning using a trial-by-trial, whereas we used a predictable rotation, blocked the conditions, instructed the participants to attend one one cursor, measured learning in an aftereffect block. An attenuation of motor responses due to the presence of irrelevant feedback has also been observed for online corrections to cursor jumps (Reichenbach et al., 2014).

One explanation behind the attenuation could be that the irrelevant information diverted visual attention from the relevant cursor, reducing adaptation. Previously, Taylor and Thoroughman demonstrated that in a force field reaching adaptation task, participants adapted less to the perturbation when performing a secondary task designed to divide attention (Taylor and Thoroughman, 2007). Given the similarity between across all the cursors, moving with the same spatiotemporal correlation and originating from the same start position, it is likely that the irrelevant cursors resulted in diverting some attention in our task (Folk et al., 1992).

The attentional explanation also provides an account for the seemingly contradictory findings sensitivity to task-relevance with multiple sources of feedback, yet inability to ignore a single cursor when participants are explicitly instructed to do so. An analogy would be with the ‘cocktail party effect’ (Cherry, 1953). When there is only one cursor on a dark background, or one person

speaking in isolation, it is difficult to ignore, whereas when there are multiple cursors, or multiple speakers, it is possible to tune-in to the most relevant one. Extending the analogy further, when tuning in to one specific speaker, the presence of other voices may be distracting, reducing the signal to noise ratio, but the exact words being spoken by the other speakers have little effect. Similarly, while we find that the additional cursors attenuated overall adaptation, the rotations of the distractor cursors appeared to have no effect.

Another possible factor contributing to the attenuation could be related to the effects of increased uncertainty of visual feedback. Intuitively, if the motor system is trying to identify visual motion related to the feedback of the movement, any other additional motion present will add noise to the process, reducing the overall signal to noise ratio and certainty of the feedback. Increasing the uncertainty of the feedback, either through blurring the feedback or displaying a cloud of cursors has been shown to attenuate responses in adaptation and online corrections (Körding and Wolpert, 2004; Burge et al., 2008; Wei, 2010). However, one qualitative difference between our study and those specifically manipulating visual uncertainty is that unlike their manipulations, the relevant cursor in our study was still a well defined circle.

Another explanation for the attenuation, based on a recent study from our laboratory (Kim et al., 2019) would be consistent with the hypothesis that implicit adaptation learns from two distinct types of errors: sensory prediction errors (SPE) and task performance errors (TE). Using a task designed to isolate implicit adaptation, we measured adaptation in response to clamped visual feedback with small angular offsets ($1.75^\circ - 3^\circ$). The angular offsets were small enough such that we could compare conditions with different target sizes, such that the same offset would result in the clamped feedback either hitting or missing the target. We found that learning was attenuated in the ‘hit’ condition compared to the ‘miss’ condition. One interpretation was that the ‘miss’ condition reflected learning from both SPE, due to the rotation of the cursor, and TE, due to the cursor missing the target. Whereas in the ‘hit’ condition, there was only learning from SPE. Consistent with this interpretation, the attenuated adaptation seen in the current experiments could solely reflect learning from TE, since it is sensitive to task relevance. Any learning from SPE would have been weakened or eliminated due to the presence of the cursor where the hand was, or the balanced rotations. The size of aftereffects observed in this manuscript is comparable to the $\sim 10^\circ$ of attenuation observed in Kim et al (2019). Although this interpretation is compatible with our results, the evidence is not conclusive since the experiments here were not designed to test this hypothesis.

Limitations and future directions

A limitation of our study is that we did not control or monitor fixation. Since it is likely that participants directed their gaze at the relevant target (Neggens and Bekkering, 2000; Rushworth et al., 2001), one might argue that participants adapting to the relevant cursor could simply be mediated by the fact that the salience of the distractor cursors is weak because of their more peripheral position. We think that a fixation-based argument is unlikely to account for the effects observed here. First, the distractor cursors attenuated adaptation in all conditions, including in

Experiment 2 where the relevant and distractor cursors were 90° apart. Thus, at least for the angular separations employed here, there is no obvious relationship between distance and attenuation. Second, prior work (Rand and Rentsch, 2015) has shown that magnitude of implicit adaptation is similar if participants are required to maintain fixation on the start position, target, or allowed to gaze freely.

An obvious follow up question as a result of our findings is at what stage in the motor control system does the filtering of relevant sensory feedback takes place? Assuming that the effects on implicit adaptation occur through effects on the SPE, it seems plausible that the relevance of the feedback could affect either how the prediction is generated or how the feedback is perceived.

Supplementary Information

For the Ignore group in Experiment 1b, we used a cluster analysis approach to identify if there were any significant clusters during training where the hand deviated from 0. This step consisted of three steps. First, a t-test was performed for each cycle, asking if the observed hand angle diverged from zero. Second, clusters were defined as epochs in which the p value from the t-tests were less than 0.05 for at least two consecutive cycles. Third, to identify the probability of obtaining a cluster of consecutive cycles with significant p values, we performed a permutation test. In this, we created 1000 permutations of the data with the cycles shuffled. For each shuffled permutation, we performed the first two steps described above to identify clusters and for those meeting this criterion, and calculated the sum of the t-scores over the significant cycles. Doing this for each of the 1000 permutations resulted in a distribution of t-scores. The proportion of random permutations which resulted in a t-score of equal or greater to that obtained from the data could therefore be directly interpreted as the p value.

Applying the first two steps to the actual data, we identified only one cluster, and only of length two (training cycle 10 mean = 2.32° [1.29°, 3.35°], $t(11) = 4.956$, $p = 4.315e-4$, $d = 1.431$, and cycle 11 mean = 1.58° [0.55°, 2.62°], $t(11) = 3.362$, $p = 0.006$, $d = 0.971$). The sum of t-scores for the two consecutive cycles ($t = 8.318$) was compared to the distribution generated by the permuted distribution, producing a p-value of 0.004. We therefore concluded that this cluster of cycles represented a significant deviation from 0, rather than being due to chance.

Chapter 3

Individual differences in proprioceptive reliability predict the extent of implicit sensorimotor adaptation

Abstract

Humans maintain calibration of their movements from visual and proprioceptive feedback, a process known as sensorimotor adaptation. Studies using visual perturbations to induce adaptation have revealed an upper bound on this process, beyond which changes in performance require alternative learning processes. The factors determining this limit are poorly understood. One hypothesis, inspired by models of multisensory integration, is that the limit arises from opposing responses to visual and proprioceptive feedback. As individuals adapt movements to a visual perturbation, they experience an increasing proprioceptive error in the opposite direction. The point at which the response to these two signals reach equilibrium may determine the limit of implicit adaptation. Assuming that visual and proprioceptive feedback are weighted according to their reliability, a reduction in the reliability of proprioceptive information should increase the upper bound of implicit sensorimotor adaptation. Here we test this hypothesis by considering natural variation across individuals, asking if there is a correlation between individual differences in proprioceptive acuity and the extent of visuomotor adaptation. We first established that individual differences in adaptation to a visuomotor rotation and proprioceptive acuity were reliable across days. Having established this, we compared the two measures and observed a negative correlation between proprioceptive acuity and the extent of implicit adaptation, consistent with the sensory integration hypothesis. We obtained a similar correlation in a second experiment in which a visual clamp was used to induce adaptation, a method that ensures adaptation is implicit. Together, our results suggest that a participant's proprioceptive reliability is a significant factor in predicting the upper bound in implicit adaptation to a visual error, consistent with a multisensory integration model of human motor learning.

Introduction

Accurate motor control requires constant calibration of the sensorimotor system, a process driven by the sensory feedback experienced as a result of movement. One of the primary learning processes involved in maintaining this calibration is known as implicit adaptation (Krakauer et al., 2000; Tseng et al., 2007; Shadmehr et al., 2010; Taylor et al., 2014). Here, learning is driven by the difference between the predicted feedback from a movement and the actual sensory feedback. This error signal is known as a sensory prediction error, or SPE.

Recent findings have shown that implicit adaptation in responses to a visuomotor rotation is remarkably invariant across a large range of error sizes and tasks (Morehead et al., 2017; Kim et al., 2018). Although participants are capable of compensating for large perturbations (e.g., rotations of 45° or 90°), this is achieved through by employing explicit aiming strategies to bolster the changes made possible via implicit adaptation (Taylor et al., 2014; Bond and Taylor, 2015; Morehead et al., 2015). Aiming allows for rapid learning (Taylor et al., 2014; McDougale et al., 2015) and is flexible (Taylor and Ivry, 2011), although it is resource demanding (Haith et al., 2015; Huberdeau et al., 2015; McDougale and Taylor, 2019). Implicit adaptation on the other hand, is involuntary (Mazzoni and Krakauer, 2006; Taylor and Ivry, 2011), learns slowly, and is typically limited to 15°-25° of learning, regardless of the size of rotation (Bond and Taylor, 2015; Morehead et al., 2015).

Converging evidence for the limitation of implicit adaptation comes from experiments using a visual error clamp. With this method, participants reach towards a target and receive visual feedback of a cursor that is temporally correlated with their hand position, but restricted to a fixed path, deviating from the target by a constant angular offset. Participants are fully informed about the invariant nature of the feedback and told to ignore it. Despite this knowledge, they implicitly adapt to the feedback, with the hand angle deviating in the opposite direction of the clamp. Interestingly, the asymptote observed in response to the clamped feedback shows a similar upper bound as that associated with implicit adaptation in response to standard visuomotor rotations (Bond and Taylor, 2015; Morehead et al., 2017). Indeed, while the initial rate of learning varies with clamp size, at least for small clamp offsets (<6°), the asymptotic limit of implicit adaptation is near-identical across all angular offsets (Kim et al., 2018).

The clamp method has the additional feature of revealing individual differences in the magnitude of adaptation. In standard adaptation studies, the asymptote is constrained to a large extent by the task goal: That is, the combination of adaptation and other learning processes are typically sufficient to compensate for the perturbation. As such, there is modest between-participant variance in terms of the asymptotic value. In contrast, there is no task goal with the clamp method and the error signals remain invariant. Asymptotic values here are reflective of the responsiveness of the adaptation system to the clamp. Studies using the clamp method have shown considerable variability between participants. For example, in one study (Kim et al., 2018), the range of asymptotes in response to a 15° clamp was between 12° and 43°. In general, the between-subject variability is similar to different clamp sizes.

The factors which determine the limits of implicit adaptation are poorly understood. One hypothesis is that the limit reflects the interaction of visual and proprioceptive feedback. In visuomotor rotation experiments, the visual feedback is rotated to produce a visually-based sensory prediction error (SPE). As adaptation progresses, the hand movements are adjusted away from the target, thus reducing the visual SPE. However, this results in an increase in a proprioceptive sensory prediction error, the difference between the expected and experienced signals of hand position. The direction of the proprioceptive SPE is opposite to that of the visual SPE, and thus the response to these two SPEs are in the opposite directions. The asymptotic level of adaptation may reflect an equilibrium between learning from visual and proprioceptive error signals.

Studies of multisensory integration have shown that when participants estimate the location of their hand, they use a combination of visual and proprioceptive feedback, weighting each source in proportion to their inverse variances (van Beers et al., 1999, 2002; Ernst and Banks, 2002; Sober

and Sabes, 2003). In the context of visuomotor adaptation, the response to a visual perturbation is reduced when noise is added to the visual feedback (Burge et al., 2008; Wei, 2010). The corollary prediction, namely that the response to a visual perturbation would increase if noise is added to proprioceptive feedback, has not been tested, likely because it is technically more challenging to manipulate proprioceptive feedback.

An alternative approach is to exploit the natural variations between individuals in their sensitivity to proprioception, asking if these individual differences are predictive of the magnitude of the response to a visual perturbation. Specifically, if a participant has a less reliable sense of proprioception, they should give a larger weighting to the visual errors and therefore reach a greater level of implicit adaptation. Here we test this sensory integration hypothesis in two experiments, examining the relationship between individual differences in proprioceptive acuity and implicit adaptation. To operationalize proprioceptive acuity, we used a psychophysical procedure to estimate the participants' reliability in estimating the position of their hand after passive displacement. The upper bound on implicit adaptation was estimated by measuring the participants' aftereffect in response to a visuomotor rotation in Experiment 1 and asymptotic response to a visual clamp in Experiment 2. Correlations between measures are only meaningful if each measure is itself reliable. Thus, participants in Experiment 1 task were tested in two separate sessions to obtain measures of test-retest reliability.

Methods

Participants

Undergraduate students were recruited from UC Berkeley's participant pool (age, male/female) and financially compensated for their participation in the experiment. All participants were right handed as assessed by the Edinburgh handedness inventory (Oldfield, 1971) and provided written, informed consent.

Experimental overview

Both experiments consisted of a mix of reaching trials and proprioceptive probes. For both tasks, participants were seated in front of a custom table top setup. On reaching trials, the movements were made by sliding a digitizing pen, embedded in a custom handle, across a graphics tablet (49.3 cm by 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA, sampling rate=200 Hz.). On proprioceptive trials, the participant held the digitizing pen and the experimenter moved the participant's arm. In both phases, the participant's view of their hand was occluded by a LCD monitor (53.2 cm by 30 cm, ASUS), horizontally aligned and positioned above the tablet. The room lights were extinguished to minimize peripheral vision of the arm.

Reaching Trials: Participants performed 16 cm reaches from a white ring (6 mm diameter), the start location, to a target (variable locations, see below) indicated by the position of a blue circle (6 mm). To initiate a reaching trial, the participant was required to move their hand within 6 mm of the start position. Visual feedback of the hand position was given via a cursor (white circle 3.5 mm diameter) only when the hand was within 1 cm of the start position. Participants were

instructed to perform ‘shooting’ movements, making a rapid movement that intersected the target (e.g., discourage on-line corrections). There were two types of feedback trials, where the cursor remained visible throughout the reach, up until the target radial distance. On veridical trials, the cursor corresponded to the position of the hand. On perturbation trials, the cursor was either rotated relative to the hand position (visuomotor rotation, experiment 1) or restricted to an invariant path along a constant angle with respect to the target (visual clamp, experiment 2). On no-feedback trials, the cursor was removed when the target appeared, and did not re-appear until the participant had completed the trial and was near the start position for the next trial. All trials were subject to the same movement time constraints, defined as the time between when the hand exceeded 1 cm from the start position to the target distance (16 cm). If movement time exceeded 300 ms, the computer generated a sound saying “too slow”. If the movement time was less than 300 ms, a neutral ‘knock’ sound was generated. There were no constraints on reaction time.

Proprioceptive Probe Trials: To probe proprioceptive acuity, the experimenter sat across the participant on the opposite side of the table. From this position, the experimenter could passively move the participant’s right hand to different probe locations (see below). The participants were instructed to hold on to the digitizing pen at all times, but to do so passively, such that they were never actively moving their hand. The experimenter kept her left hand on the participant’s hand throughout the proprioceptive probe block.

The experimenter initiated each trial by moving the participant’s hand into the start position. Once within 1 cm of the start position, the word ‘Ready’ appeared on the screen. The experimenter then hit the space bar with her right hand, at which point a number corresponding to the target position was displayed to the experimenter on the corner of the monitor closest to the experimenter (Figure 1). A small cover placed on the corner of the monitor prevented the participant from being able to see the number. The experimenter then moved the participant’s hand to the specified target location. Once the participant’s hand was within 2 cm of the target location, the word ‘Ready’ again appeared on the screen and the experimenter hit the space bar to advance the trial. A filled white circle (3.5 mm diameter) then appeared in a random position on the monitor. The participant moved a mouse (Logitech Trackman Marble) with their left hand to position the cursor above the felt position of their right hand. When satisfied with the position of the cursor, the participant clicked the mouse button. The participant was free to modify their response by repositioning the mouse and clicking again. After the experimenter confirmed that the participant had completed the trial, the experimenter hit the space bar at which point the cursor disappeared. The experimenter moved the participant’s hand back to the start position in order to initiate the next trial. The start position remained on the screen for the entire duration of the proprioceptive probe trials. We opted to use a tolerance window of 2 cm in positioning the hand, using a value that was large enough for the experimenter to guide the participant’s hand to the target location without feedback, and small enough to ensure variation in target positions across trials. Variance in the positioning of the hand was irrelevant given that the responses were recorded relative to the actual position, not the target position.

Experiment 1

In experiment 1, we used a 30° visuomotor rotation to assess the relationship between the extent of implicit adaptation and proprioception. We performed a two-day experiment with the same

protocol so that we could also assess the test-retest reliability of our measures of adaptation and proprioception.

Reaching and proprioceptive trials were performed to 5 targets located within a forward wedge (at 70°, 80°, 90°, 100°, 110°). The trials were arranged in cycles of one trial per target, with the order randomized within a cycle. The experiment began with a brief phase to familiarize the participants with the reaching task. This consisted of 10 baseline reaching trials in which no visual feedback was provided, followed by 10 baseline trials with online feedback. During the latter, the participant was instructed to hit the target with the cursor using a shooting movement. The cursor remained visible throughout the movement and disappeared immediately after it exceeded the target radial distance.

Following the familiarization phase, the participant completed a block of 50 baseline proprioceptive probe trials. After this, the participant switched back to reaching with feedback, but unbeknownst to the participants, the cursor was rotated relative to the true hand position. To minimize awareness, small, incremental steps were imposed with the rotation increased by 0.33° per trial up to 30° over 90 trials. Across participants, we counterbalanced the direction of the rotation (clockwise or counterclockwise).

The participant then completed 7 more blocks, alternating between proprioceptive probe trials (30 per block) and reaching trials (40 per block, at the full 30° rotation). With this alternating schedule, we sought to obtain measures of changes in proprioception from adaptation while minimizing potential effects of forgetting or washout of the adaptation (Cressman and Henriques, 2009). Intermixed with the alternating blocks, participants performed four blocks of 5 no-feedback trials in which they were instructed to reach directly to the target. The blocks occurred after the first gradual perturbation block, the second fixed perturbation block, the third perturbation block, and the fourth proprioceptive probe block. These aftereffect data provided our primary measure of adaptation and were used to assess its time course. To complete the session, the participants completed 50 reaching trials with veridical feedback to ensure that the residual effects of adaptation were removed.

Each participant returned for a second session, 2 to 14 days after the first session. The experimental protocol was identical on day 2 for each participant.

Experiment 2

We used the visual clamp method in experiment 2 as an alternative method to obtain an upper bound on implicit adaptation for each participant. A potential advantage of this type of perturbation for the task is that there is greater variability between participants. Based on the inter-individual reliability results from experiment 1, we did not believe it was essential to perform this as a two-day experiment and instead performed it as a one-day experiment. Aside from using clamped feedback rather than a visuomotor rotation, other changes (discussed below) were made to the experimental procedure in an attempt to improve the quality of proprioceptive estimates.

Although participants were not explicitly asked in experiment 1, we suspected that some participants were aware that there were 5 discrete target locations. The concern was that if this were the case, on the proprioceptive trials they may report a remembered a previously reported hand position associated with the target location, rather than relying on their proprioceptive sense

alone. Therefore, we used a finer sampling of the same space as a precautionary measure to reduce the participant's ability to perceive the presence of discrete target locations. The targets were spaced every 5° instead of every 10° (70°, 75°, 80°, 85°, 90°, 95°, 100°, 105°, 110°).

Unlike experiment 1, experiment 2 began with one cycle (1 trial per 9 targets) of proprioceptive probes. Other than the target locations, the proprioceptive probes used the same method as experiment 1. This block was not further analyzed and was used solely to familiarize the participant with the procedure during proprioceptive trials. The change was made so that participants could familiarize themselves with the procedure and ask questions before data was collected for the baseline proprioceptive block, where they would then be able to focus solely on using estimating their hand position.

Participants then performed 27 reaching trials with no feedback to 9 targets, followed by a block of 72 baseline trials with online feedback. There was a break half way through the feedback block. The targets covered a wider range than in experiment 1, spanning 50°-130°, spaced 10° apart from each other. In unpublished error clamp experiments from our lab, when using a single target we would occasionally observed non-monotonic adaptation profiles with adaptation initially increasing, then decreasing. In order to reduce this unknown effect, and to observe implicit learning profiles similar to those obtained in previously published error clamp studies using 8 targets around the workspace, we used a wider range of targets. Since this experiment used 16 cm reaches rather than 8 cm reaches, and given the size limitations of the tablet, the span of 50°-130° was chosen. After the baseline reaching block, participants performed 72 proprioceptive probe trials with a break half way through.

The participant then completed an error clamped feedback blocks of 180 trials with a break half way through. On these trials, the cursor was constrained to a straight path which was offset 15° away from the target. The radial distance of the cursor from the start position matched that of the participant's hand. As a result, the motion of the cursor was temporally correlated with the participant's hand, but its direction would be fixed, independent of the participant's hand angle. Just before the block, participants were told about the invariant feedback and instructed to ignore it, thus, minimizing the contributions from explicit aiming strategies (Morehead et al., 2017; Kim et al., 2018). To help participant understand the task, they were given three demonstration trials where they could experience the invariant nature of the feedback (Kim et al., 2018, 2019). On all three trials, the target appeared straight ahead at 90°. On each trial, participants were told to reach away from the target. On the first, second and third trial, respectively, they were instructed to reach to the left, to the right, and backward. On each trial, the cursor would move in a straight line 15° away from the target, allowing the participant to see that it was unrelated to their own reach direction. The experimenter then confirmed with the participant that they understood the feedback and the task before proceeding with the clamped feedback block. Then, participants completed 7 alternating blocks of 36 proprioceptive trials and 90 error clamped blocks.

Dependent variables

Our hypotheses were concerned with two variables of interest: implicit adaptation, proprioceptive reliability. The primary variable for assessing implicit adaptation was the change in hand angle from baseline, where the hand angle was defined as the signed angular difference between the position of the hand at peak velocity and the target angle. In experiment 1, we assessed implicit

adaptation using the mean hand angle during no-feedback aftereffect trials in experiment 1. In experiment 2, we used the mean hand angle during the last block of error-clamp trials. Values reported in the figures and statistics are baseline-subtracted, where the baseline for each experiment was defined as the mean hand angle over the last two cycles of feedback baseline trials.

For our measure of proprioception, we calculated the mean and variability of the location reports for each block. The mean centroid was calculated by taking the mean x and y coordinate of each location report. Our primary interest was the proprioceptive variability, defined as the mean Euclidean distance of each location report to the mean centroid. Our central question was whether proprioceptive variability would be predictive of the extent of implicit adaptation. Therefore we used the proprioceptive variability from the baseline trials, before being exposed to the perturbation, as our primary variable of interest. As a secondary interest, we were also interested in the proprioceptive shift, defined as the change in the mean centroid from baseline to each block.

For proprioceptive reliability, for each participant we used trials from their baseline proprioception block to calculate the mean Euclidean distance (in mm) between each proprioceptive estimate and the centroid.

Previous work on sensorimotor adaptation and proprioception have shown that reaching with perturbed visual feedback can induce a recalibration in proprioceptive sense, a proprioceptive ‘shift’, as well as a recalibration of reaching behavior (Block and Bastian, 2009; Cressman and Henriques, 2009, 2010). Since the main hypothesis was based with the relationship between visual and proprioceptive feedback, a recalibration of proprioceptive feedback would be of primary importance. For example, it could be possible that an individual’s extent of proprioceptive shift could be correlated with their extent of implicit adaptation. To quantify the proprioceptive shift, we measured the change in proprioceptive bias relative to baseline, where the proprioceptive bias for each block was defined as the angle between the centroid of proprioceptive estimates, the start position and the target.

Data Analysis

One trial in which the hand angle exceeded 90° was excluded from the analysis. The experimental software and analysis were performed using custom scripts in Matlab, using the Psychtoolbox extensions (Pelli, 1997). All t-tests were two-tailed unless stated otherwise. For both experiments, aftereffect analyses were performed on baseline subtracted data, defined as the last 10 baseline trials in Experiment 1 and the last three error clamp cycles in Experiment 2.

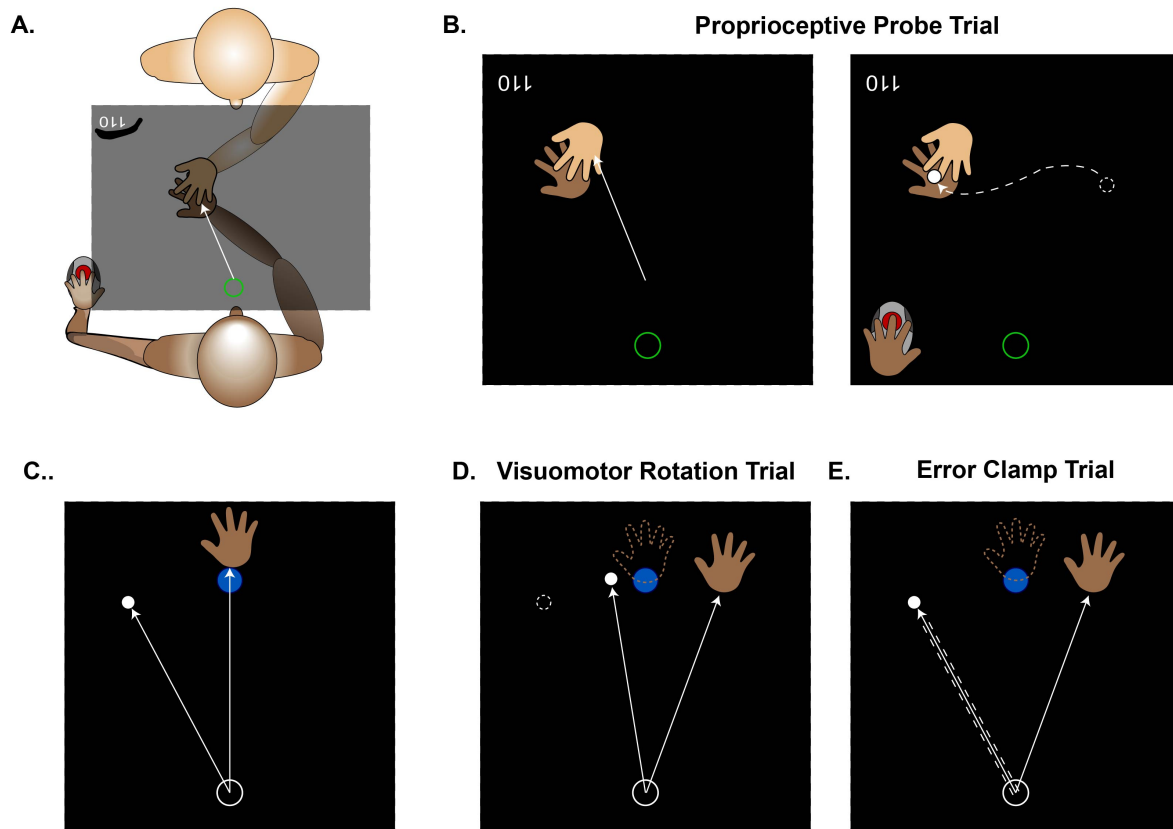


Figure 3.1 Experimental setup. A) Experimental setup for proprioceptive probe trials. The experimenter (top) sat opposite the participant (bottom) and moved their hand from the start position to a specified location. The location (e.g. 110°) was signaled to the experimenter via text which appeared on the corner of the horizontal monitor, behind a cloth which shielded it from the participant. B) After the participant's hand was passively moved to the probe location, a cursor appeared at a random position on the screen. The participant was then instructed to move the cursor to their felt hand position, using their left hand to control a rollerball mouse. C) Example visual perturbation on a reaching trial. D) In Experiment 1, a rotation was applied to the cursor such that the participant could compensate for it by moving their hand in the opposite direction to the perturbation. E) In Experiment 2, the cursor was clamped such that a change in hand angle would not result in a change of the cursor trajectory. Participants were informed about the clamped feedback and told to ignore it and to aim straight for the target.

Results

Experiment 1

Experiment 1 had two aims. First, to assess the stability of individual differences of our main dependent variables: implicit adaptation, proprioceptive reliability, and proprioceptive recalibration. Second, to test the multisensory integration model by determining whether there was a correlation between proprioceptive variability and implicit adaptation. To achieve this, we performed a two-day visuomotor adaptation experiment intermixed with proprioceptive probe blocks ($n = 30$). To induce implicit adaptation, we imposed a gradual visuomotor rotation on the cursor at a rate of 0.33° per trial, up to 30° . The limit of 30° was based on previous experiments showing that the limit of implicit adaptation is on average around 15° - 25° .

In order to assess the time course of adaptation, we used multiple cycles of reaching trials and proprioceptive trials. The first aftereffect cycle of reaching without feedback occurred immediately after the gradual rotation had reached 30° . A *t*-test revealed that the mean hand angle was significantly different from zero (AE1 mean = 19.7° , $t(29) = 24.612$, $p < .001$) (Figure 2B). The next aftereffect block occurred after two more training blocks with the 30° rotation. A paired *t*-test revealed that the second aftereffect was greater than the first (AE2 mean = 24.0° , difference = 4.2° , $t(29) = 5.869$, $p < .001$), showing that implicit adaptation had not reached its limit within the first aftereffect cycle. The third aftereffect block (AE3) was not significantly different from the second (AE3 mean = 23.6° , difference = -0.4° , $t(58) = -0.651$, $p < .001$), suggesting that participants had reached their limit of implicit adaptation. Furthermore, the fact that this extent of adaptation was similar to those seen in previous studies (Bond and Taylor, 2015; Kim et al., 2018, 2019) meant we were in a position to assess whether the limits of adaptation were related to proprioceptive reliability. The final aftereffect cycle (AE4) occurred immediately following a proprioceptive probe block and was used to determine whether the proprioceptive blocks were washing out implicit adaptation. AE4 was still significantly different to zero (AE4 mean = 18.5° , $t(29) = 23.331$, $p < .001$), meaning that adaptation had not been completely washed out. However, it was less than AE3 (difference = -5.1° , $t(58) = -7.803$, $p < .001$), showing that there was some washout of implicit adaptation during the proprioceptive probe block.

Day 2 had overall lower aftereffects than day 1. However the overall pattern was similar. Aftereffect blocks two and three were not different (Day 2 AE2 mean = 18.9° , AE3 mean = 19.5° , difference = 0.6° , $t(58) = 0.474$, $p = 0.637$), suggesting that participants reached their limit of adaptation. Also, aftereffect block four was lower than aftereffect block three (Day 2 AE4 mean = 14.3° , difference = -5.2° , $t(58) = -3.697$, $p < .001$), showing that the proprioceptive blocks caused some washout of implicit adaptation. It is possible that the error experienced during washout trials could have influenced participants' behavior on the next day, however, the average error on the first cycle was less than 20° , where the contributions of explicit strategies is minimal (Bond and Taylor, 2015; Morehead et al., 2015).

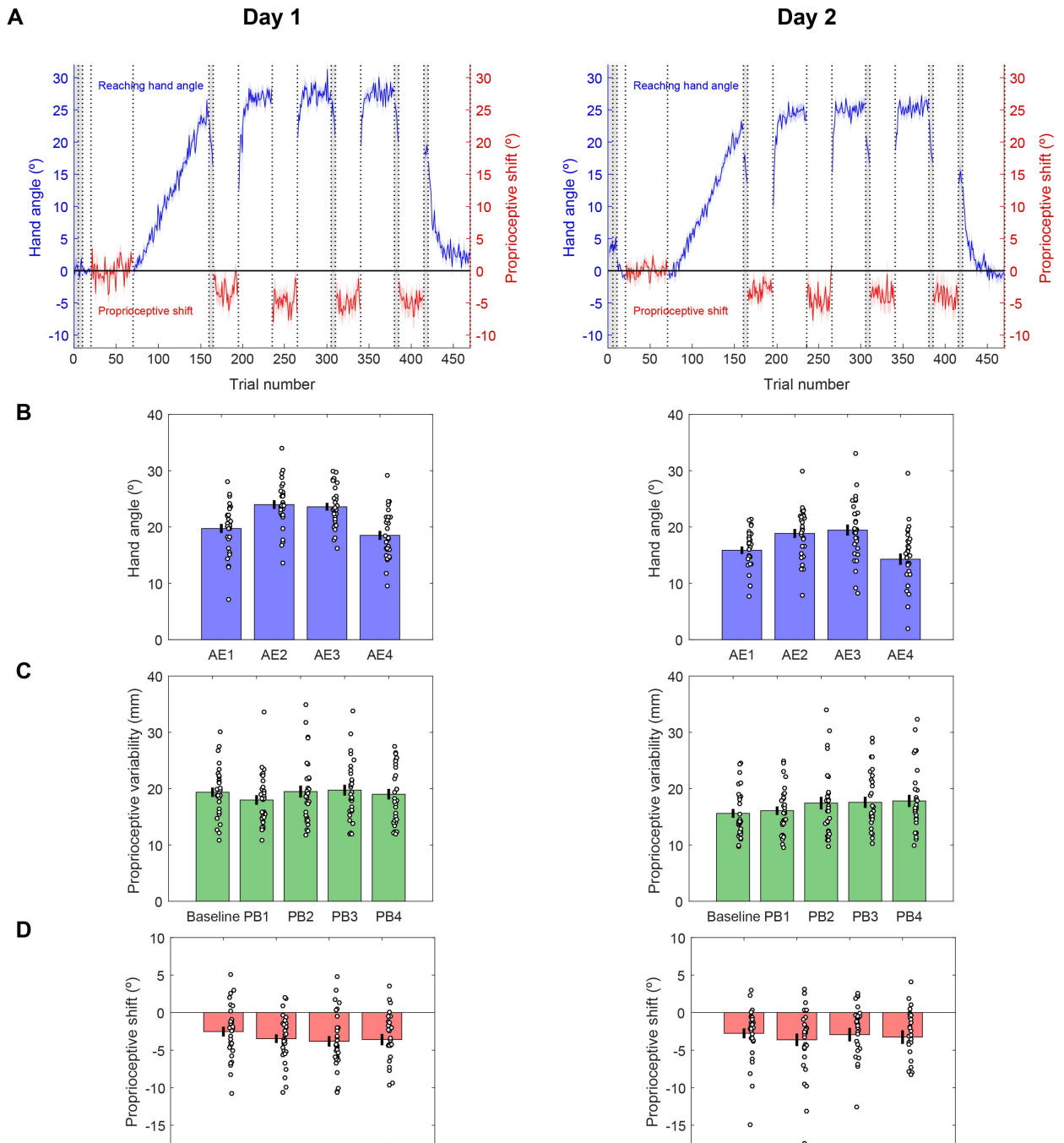


Figure 3.2 Experiment 1 Group Average behavior. Left – Day 1, Right – Day 2. A. Group means for reaching and proprioceptive trials. After a period of baseline trials, participants were exposed to a gradually increasing visuomotor rotation up to 30°, where it was then held constant. Participants performed blocks of reaching trials (Blue) and proprioceptive probe trials (Red). Vertical dotted lines indicate block breaks and shaded trials indicate reaching trials with no feedback. Shaded regions indicate ± 1 SEM. B. Group mean hand angles during no feedback Aftereffect blocks. C. Proprioceptive shift relative to the baseline proprioceptive block. D. Proprioceptive shifts for each proprioceptive block, relative to baseline. Circles indicate individual subjects and black lines indicate ± 1 SEM.

For defining proprioceptive reliability, we quantified the mean Euclidian distance (in x and y coordinates) from each proprioceptive estimate in the block to the centroid. Figure 2 shows the mean proprioceptive variability for each proprioceptive block for each day. A one way repeated measures Anova revealed no effect of block for day 1 ($F(4,116) = 1.708, p = 0.153$), however, there was an effect of block for day 2 ($F(4,116) = 3.440, p = 0.011$). This was driven by the proprioceptive variance increasing over the blocks in day 2. Post-hoc ttests revealed significant differences were between the baseline block and the last block ($t(29) = -2.181, p = 0.037$), and second to last block ($t(29) = -2.163, p = 0.039$).

Previous studies have shown that perturbed visual feedback can cause proprioceptive shifts (Block and Bastian, 2009; Cressman and Henriques, 2009, 2010). Since the hypothesis of implicit adaptation reaching a limit is based on an equilibrium between visual and proprioceptive SPE, it's possible that inter-individual in proprioceptive shifts could correlate with the extent of implicit adaptation. Also, since the proprioceptive shift would itself be the result of learning from the visual feedback, we may expect it to be correlated with proprioceptive reliability. To address these related hypotheses, we assessed whether the rotation had resulted in proprioceptive shift.

To assess proprioceptive recalibration, we quantified the proprioceptive shift as the angular change in the centroid of proprioceptive estimates relative to the baseline block. On both days, participants exhibited a significant proprioceptive shift in the expected direction, where participants estimated their hand position as being closer to the rotated cursor during reaching trials. Each proprioceptive block following the perturbation showed a significant shift from baseline (PB1 mean = $-2.5^\circ, t(29) = -3.915, p < 0.01$, PB2 = $-3.5^\circ, t(29) = -6.037, p < 0.01$, PB3 = $-3.8^\circ, t(29) = -5.503, p < 0.01$, PB4 = $-3.6^\circ, t(29) = -4.786, p < 0.01$). However, the magnitude of this shift did not show a significant increase over the course of the adaptation trials. A one-way repeated measures ANOVA revealed no effect of proprioceptive block number on proprioceptive shift ($F(3,87) = 2.015, p = 0.118$). Similar results were obtained for day 2, where ttests revealed that each proprioceptive block had a significant shift relative to baseline (PB1 mean = $-2.8^\circ, t(29) = -4.202, p < 0.01$, PB2 = $-3.6^\circ, t(29) = -4.364, p < 0.01$, PB3 = $-2.9^\circ, t(29) = -3.273, p < 0.01$, PB4 = $-3.3^\circ, t(29) = -3.580, p < 0.01$). A one way repeated measures anova also revealed no effect of block on proprioceptive shift ($F(3,87) = 0.986, p = 0.403$). Despite using different methods, these magnitudes of proprioceptive shifts were comparable to the 3.9° proprioceptive shifts observed by Ruttle et al (Ruttle et al., 2016).

Day 1 vs Day 2 Reliability

Analyses which involve correlating measure individual differences across different measures are limited by the reliability of each measure. Therefore, before performing a correlational analysis between individual differences in proprioceptive variability and implicit adaptation, we first assessed whether individual differences in these measures were stable over days (Figure 3A). For our measure of the extent of implicit adaptation, we used the mean baseline-subtracted aftereffect from aftereffect blocks 2 and 3 as implicit adaptation appeared to have reached its limit by these blocks. For proprioceptive reliability, we used the proprioceptive variability obtained from the baseline block so that the measure would not be contaminated by any changes which may have occurred during the perturbation trials. For proprioceptive shift, we used the mean proprioceptive shift of all blocks relative to baseline. All three dependent variables revealed significant between-participant correlations from day 1 to day 2 (implicit adaptation, $r = 0.569, p = 0.001$;

proprioceptive reliability, $r = 0.563$, $p = 0.001$; proprioceptive shift, $r = 0.499$, $p = 0.005$), indicating that the individual differences were stable and measurable.

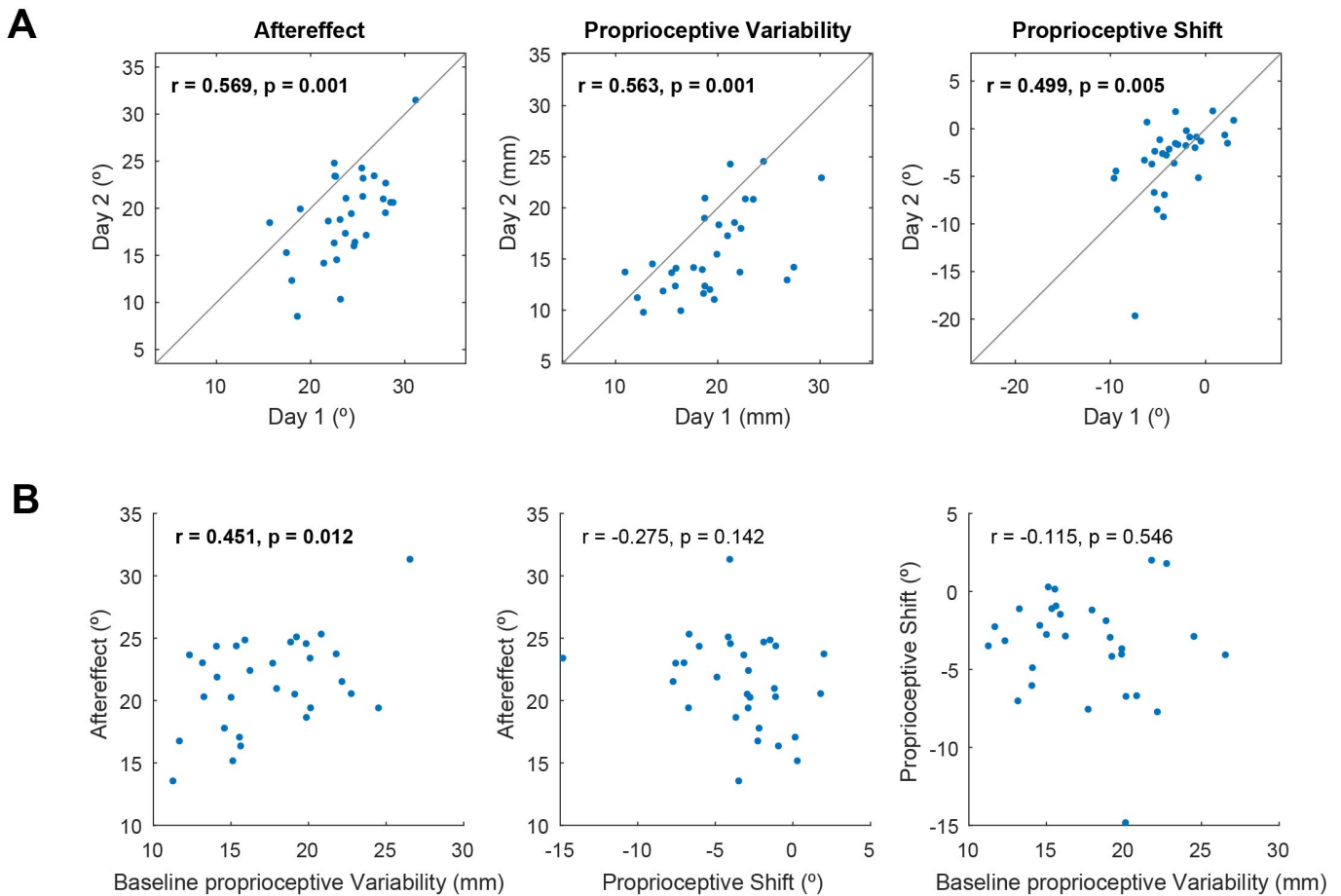


Figure 3.3 Experiment 1 Inter-individual differences results. A) reliability of individual differences across both days. Left: Aftereffects, Middle: Proprioceptive variability, Right: Proprioceptive shift. B) Correlations of individual differences. Left: Baseline proprioceptive variability vs aftereffect. Middle: Proprioceptive shift vs aftereffect. Right: Baseline proprioceptive variability vs proprioceptive shift.

Having established that these dependent variables were reliable across days, we next asked whether differences in implicit adaptation could be accounted for by differences in proprioceptive shifts or proprioceptive variability.

Correlations between Adaptation and Proprioception

Figure 3 shows correlations between the three dependent variables. The one of primary interest is the correlation between baseline proprioceptive reliability and aftereffect. According to the multisensory integration hypothesis, since vision and proprioception are weighted according to the reliability of their signals, we should expect a negative correlation between proprioceptive

reliability and extent of adaptation. A correlational analysis between these two measures revealed a significant correlation in the expected direction ($r = 0.451$, $p = 0.012$). This result demonstrates that differences in proprioceptive reliability can predict the extent to which a participant adapts. This supports the multisensory integration account for explaining the limit of implicit adaptation, that it represents an equilibrium between learning from visual and proprioceptive SPEs.

Since both implicit adaptation and proprioceptive recalibration are driven by visual sensory prediction errors, we might have also expected to find that individual differences in the extent of these effects would be correlated. Since implicit adaptation drives reaching in the opposite direction to the visual perturbation (in order to compensate for it), and proprioceptive recalibration shifts towards the perturbed visual feedback, we would predict the correlation to be negative. The correlation was negative but not significant ($r = -0.275$, $p = 0.142$) (Figure 3B).

Finally, the multisensory integration model would also predict that the amount of proprioceptive recalibration would be influenced by the relative weighting of proprioception and vision. For a motor system with relatively noisier proprioception, the proprioceptive feedback should be 'trusted' less, and therefore be more amenable to recalibration. If this were the case, we would expect a greater proprioceptive variability to result in a greater proprioceptive shift. While the correlational analysis between proprioceptive variability and proprioceptive shift was in the expected direction, the correlation was not significant ($r = -0.115$, $p = 0.546$).

Experiment 2

In experiment 2 ($n = 32$) we provided a second test of the multisensory integration hypothesis using a visual error clamp. The advantage of this method is that the error participants experience is held constant, independent of performance, meaning that there would be a greater potential to observe individual differences in implicit adaptation.

Figure 4 shows the reaching behavior from the error clamp feedback. Adaptation appeared to be stable across the last three clamped blocks, indicating that participants had reached their limit of adaptation. A one-way repeated measures ANOVA did not produce a significant effect of block on hand angle ($F(2,62) = 2.040$, $p = 0.139$). To obtain a single measure of adaptation for each participant, we took their mean hand over the last three clamped feedback blocks. Surprisingly, the mean asymptotic hand angle (17.4°) was slightly lower than the aftereffects in experiment 1. As expected however, the range of hand angles between participants was a lot wider, over 60° in experiment 2 compared to about 25° in experiment 1.

Although the mean proprioceptive shift after the perturbation blocks was in the right direction, it was not significantly different from baseline (mean = -1.7° , $t(31) = -1.627$, $p = 0.114$). Unlike experiment 1 and previous experiments which have induced proprioceptive shifts in participants, this one was performed with clamped feedback, in which participants are instructed to ignore the feedback. This, as well as less constrained nature of the reaching task may have been a relevant factor in inducing less proprioceptive recalibration.

For proprioceptive reliability, we used the same method as in experiment 1, taking the mean distance of each proprioceptive estimate to the centroid of that block. A one-way repeated measures ANOVA revealed a significant effect of block on proprioceptive variability ($F(4,124) = 3.811$, $p = 0.006$). Post-hoc ttests showed that the baseline variability was significantly greater than

both the last proprioceptive block ($t(31) = 3.238, p = 0.003$) and the second last proprioceptive block ($t(31) = 2.913, p = 0.007$). Overall, the baseline proprioceptive variability in experiment 2 was greater than on day 1 in experiment 1 (experiment 1: 24.3 mm, experiment 2: 19.4 mm, difference: - 4.9 mm, $t(60) = - 3.121, p = 0.003$). We note that a different experimenter had performed experiments 1 and 2. Given the interaction between the experimenter and the participants, this may have been a factor in the differences in proprioceptive variability between experiments 1 and 2.

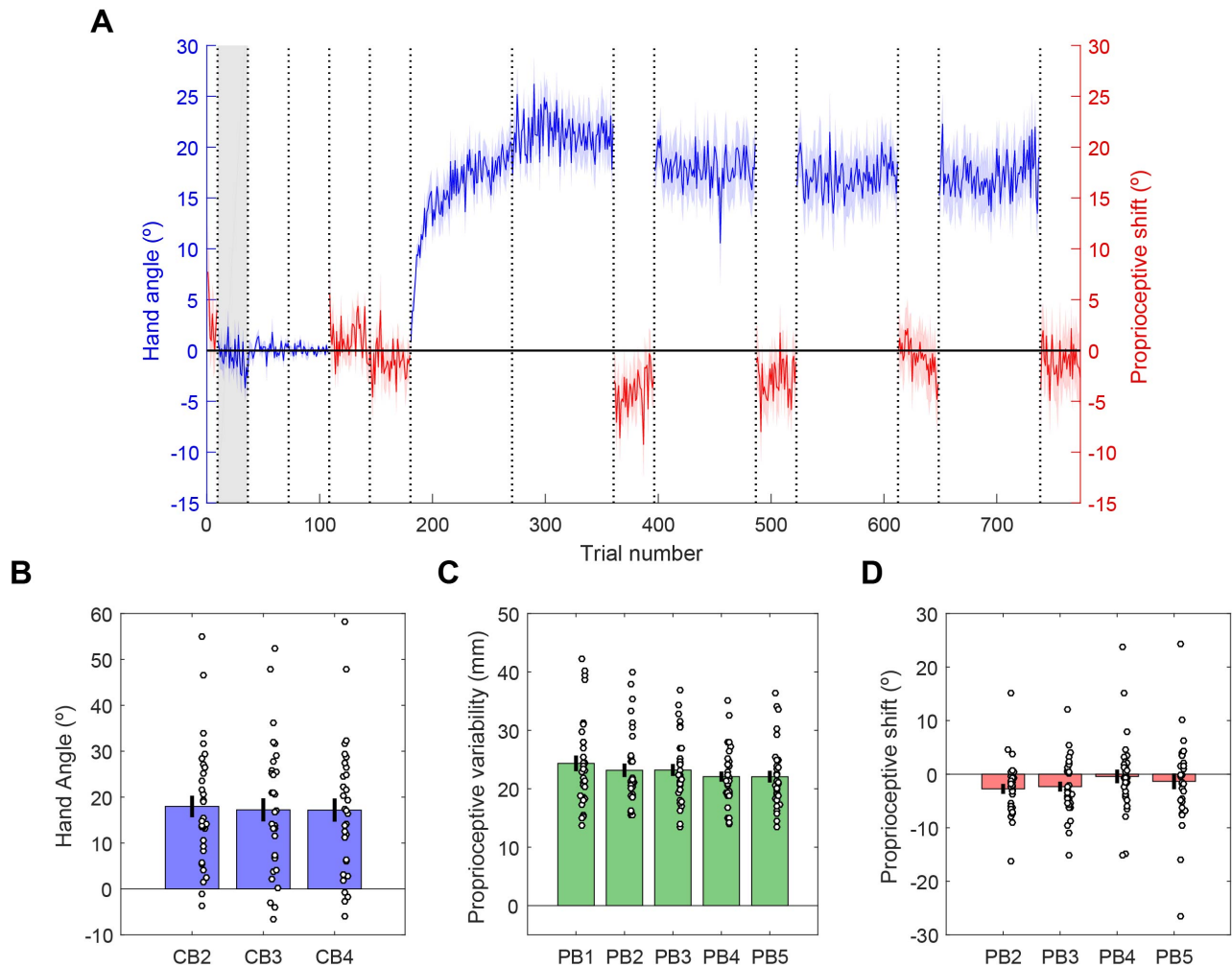


Figure 3.4 Experiment 2 results. A) Experiment 1 Group Average behavior. Blue – Hand angle Red – Proprioceptive biases. Vertical dotted lines indicate block breaks and shaded trials indicate reaching trials with no feedback. Shaded regions indicate +/- 1 SEM. B) Mean hand angles for the last three clamped feedback blocks. C) Mean proprioceptive shift for each proprioceptive block relative to baseline. D) Proprioceptive variability for each proprioceptive block including baseline.

Using the same analyses as in experiment 1, we performed a correlational analysis for each of our three dependent variables (Figure 5). Although there was a trend between the extent of implicit adaptation and proprioceptive reliability, the correlation was not significant ($r = 0.336$, $p = 0.060$). Given that the correlation was close to significance, and our overall proprioceptive variance was higher compared to experiment 1, we suspected that our estimates of proprioceptive reliability were noisy. In an effort to obtain a better estimate of the individuals proprioceptive reliability, we pooled values of proprioceptive variability across all proprioceptive blocks. In order to justify this method, we tested to see whether there was a correlation between the proprioceptive variability during the baseline block versus the blocks after the first perturbation. This revealed a very strong correlation between the two measures ($r = 0.964$, $p < 0.001$). Given this correlation, we felt it was acceptable to pool the measures of proprioceptive variability and take the participant's mean across the blocks. Using this pooled measure, we now found a significant correlation between the extent of implicit adaptation and proprioceptive reliability ($r = 0.445$, $p = 0.011$).

Unlike experiment 1, the proprioceptive shift was correlated with the amount of implicit adaptation ($r = -0.658$, $p < .001$). Also similar to experiment 1, the relationship between proprioceptive variability and the proprioceptive shift was in the predicted direction but it was not significant ($r = -0.338$, $p = 0.058$).

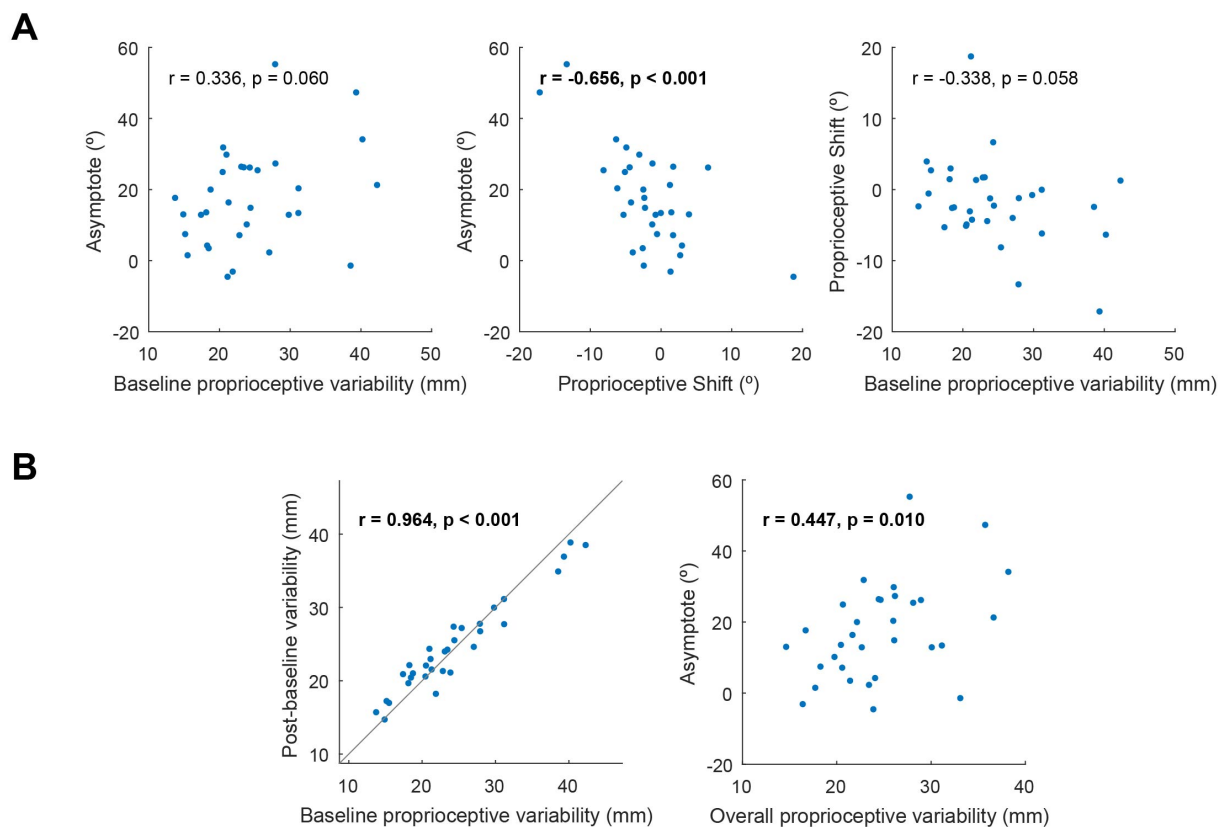


Figure 3.5 Experiment 2 results. A) Correlations of individual differences. Left: Baseline proprioceptive variability vs aftereffect. Middle: Proprioceptive shift vs aftereffect. Right: Baseline proprioceptive variability vs proprioceptive shift. B) Left: Correlation between proprioceptive variability from baseline versus post-perturbation blocks. Right: Mean overall proprioceptive variability vs aftereffect

Discussion

We sought to understand the constraints on adaptation. To achieve this, we tested whether the extent of implicit adaptation observed in sensorimotor adaptation tasks could be explained by a multisensory integration model of visual and proprioceptive feedback. By assessing participants' proprioceptive variability while performing a visuomotor adaptation task, we found that participants with a larger proprioceptive variability exhibited more implicit adaptation. This is consistent with the account that the sensory feedback is weighted according to how noisy they are: for participants with greater proprioceptive variability, their sense of proprioception was weighted less, and therefore more of their learning was driven by the visual error. This finding provides support for the multisensory integration model and also furthers our understanding on the constraints of implicit adaptation.

The question of proprioceptive variability and motor adaptation has also been studied by Lei and Wang (Lei and Wang, 2018). Their study concluded that while there was no correlation between motor adaptation and proprioceptive variability in younger adults, there was actually a negative correlation between the two in older adults. While their findings appear to be contradictory to ours, their study was focused on early learning, which previous studies have shown to be reflecting mainly explicit learning processes, especially during large, abrupt perturbations. Separate studies have shown that older adults are impaired at using explicit strategies relative to younger adults (Vandevoorde and Orban de Xivry, 2019), and that they also have more proprioceptive variability (Lei and Wang, 2018). Thus, their negative correlation in older adults could possibly be explained by two independent effects of ageing. Their lack of effect in younger adults similarly may be more reflective of a lack of correlation between the use of explicit strategies and proprioceptive variability.

A limitation of our study is that while our results are consistent with multisensory integration, our results are purely correlational and thus, we cannot necessarily infer causality. While it is possible that a third, more general process, such as alertness or motivation could have been driving both of these effects, it would be unusual for a global factor to make participants worse in one task (greater proprioceptive variability), while learning more in another task (implicit adaptation). Thus while we cannot rule out other mechanisms, we believe that the multisensory integration account is the most likely.

Future studies could build upon this research by manipulating proprioceptive variability and measuring its influence on adaptation. For example, tendon vibration or blood flow restriction have been shown to reduce proprioceptive sense (Goodwin et al., 1972; Grimby and Hannerz, 1976). Similarly, one could manipulate the variability of visual feedback to see if that would influence implicit adaptation in a similar fashion. If indeed such a relationship between proprioception and adaptation exists, this could be used to help design feedback during rehabilitation to improve the rate of recovery for patients with movement disorders.

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