An associative learning account of sensorimotor adaptation

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ABSTRACT

Two influential paradigms, sensorimotor adaptation and eyeblink conditioning, have deepened our understanding of the theoretical and neural foundations of motor learning, and in particular, the role of the cerebellum. Although there has been some cross-pollination between these two lines of research, they typically operate within distinct theoretical frameworks, with the incremental updating of an internal forward model explaining adaptation, and associative learning processes explaining eyeblink conditioning. Here we ask if a unified framework might be parsimonious, directly linking sensorimotor adaptation to associative learning. Using a task that isolates implicit sensorimotor adaptation, we paired movement-related feedback with neutral auditory or visual cues that served as conditioning stimuli (CSs) to test two key signatures of associative learning-differential conditioning and compound conditioning. We observed clear Pavlovian effects in both cases: Implicit trial-by-trial changes in movement kinematics were reliably modulated by the CSs in the predicted directions. Moreover, after compound conditioning, we observed a robust negative correlation between the responses of individuals to the two elemental CSs of the compound, consistent with the additivity principle posited by the Rescorla-Wagner model of classical conditioning. Computational modelling demonstrates that these results cannot be captured by the conventional algorithm used to explain the operation of a forward model. We believe that associative learning effects in implicit sensorimotor adaptation provide a proof-of-concept for linking multiple motor learning paradigms within a similar theoretical framework.

INTRODUCTION

Sensorimotor adaptation refers to the gradual adjustment of movements in response to changes in the environment or body. Studies of human sensorimotor adaptation typically involve imposing a perturbation during reaching (Shadmehr and Mussa-Ivaldi, 1994), walking (Reisman et al., 2005), or speech (Houde and Jordan, 1998) to generate errors that drive recalibration of an existing sensorimotor map. Over numerous iterations, the adaptation process works to reduce the errors brought on by these perturbations, helping to optimize motor performance.

The primary theoretical framework used to describe adaptation is built around the engineering concept of an internal forward model (Shadmehr and Krakauer, 2008; Wolpert et al., 1995; Wolpert and Ghahramani, 2000). Here, a simulation process operating on the motor intent generates a prediction of the expected sensory outcome. This representation is compared to the actual sensory outcome and, if they are different, a sensory prediction error is generated to incrementally tune the forward model to reduce future errors.

Adaptation via sensory prediction error is considered to be an implicit form of learning. When properly isolated from other processes that contribute to learning in typical adaptation tasks, such as explicit cognitive strategies (McDougle et al., 2016), implicit adaptation appears to be curiously limited: It does not exhibit savings (Avraham et al., 2020; Haith et al., 2015; Morehead et al., 2015), is generally insensitive to both the magnitude and consistency of errors (Bond and Taylor, 2015; Hutter and Taylor, 2018; Avraham et al., 2019), and appears to be impervious to information relevant to task performance (Mazzoni and Krakauer, 2006; Morehead et al., 2017; but see Leow et al., 2018 and Kim et al., 2019). Moreover, as shown in several recent studies, implicit adaptation fails, at least initially, in producing appropriate changes in behavior in response to other simple perturbations like mirror reversals (i.e., when visual feedback is mirrored across an unseen axis with respect to the veridical limb position), a task that should be natural for a

canonical forward model to solve (Hadjiosif et al., 2020; Telgen et al., 2014; Wilterson and Taylor, 2020).

These constraints suggest that it may be appropriate to consider a simpler, model-free computational framework for understanding implicit adaptation. As a starting point, we note intriguing parallels between adaptation and another important paradigm in the study of motor learning – Pavlovian delay eyeblink conditioning. In eyeblink conditioning, an aversive air puff (unconditioned stimulus, or US) to the cornea elicits a reflexive blink (unconditioned response, or UR). The US can be repeatedly paired with a predictive conditioning stimulus (CS, such as a tone or light flash) to gradually induce a preemptive conditioned eyeblink response (CR) that, over time, will come to be elicited even when the US is withheld. Both adaptation and eyeblink conditioning are strongly associated with learning mechanisms in the cerebellum (Donchin et al., 2011; Garcia et al., 1999; Gerwig et al., 2007; Izawa et al., 2012; Kim and Thompson, 1997; J. E. Schlerf et al., 2012). In addition, although one task involves active planning (motor adaptation) and the other passive conditioning of a reflex (eyeblink conditioning), both are thought to rely on some form of prediction error (Ohmae and Medina, 2015; Rasmussen et al., 2008; J. Schlerf et al., 2012; Shadmehr et al., 2010), which needs to occur close in time to the initial prediction to produce learning (Brudner et al., 2016; Kitazawa et al., 1995; Schneiderman and Gormezano, 1964; Schween and Hegele, 2017). Lastly, both adaptation and eyeblink conditioning can proceed outside of conscious awareness (Clark et al., 2002; Clark and Squire, 1998; Mazzoni and Krakauer, 2006; Morehead et al., 2017).

Motivated by these similarities, we ask here how one might forge more direct links between motor adaptation and eyeblink conditioning. Consider first the unconditioned events: The air puff to the cornea and the imposed perturbation in adaptation studies can both be viewed as salient USs, aversive sensory events that should be avoided or attenuated. Similarly, the eyeblink and corrective feedback responses to a volitional action can be viewed as URs, automatic actions

made in response to their respective USs. When the US becomes predictable (i.e., when paired with a CS), the output of the system is modified to produce a response that marches forward in time, eventually resulting in an adaptive, feedforward response. In this light, sensorimotor adaptation can be seen as echoing the UR-to-CR transition in eyeblink conditioning (Albert and Shadmehr, 2016), with CRs defined as feedforward adjustments of movements in response to CSs. As such, sensorimotor adaptation could in theory come about via a simple associative learning rule rather than a multi-step process that requires internal simulations to generate a sensory prediction, compare that prediction to observed sensory feedback, and then use the difference to update the forward model.

In eyeblink conditioning, a neutral sensory stimulus is introduced as the CS, and learning requires that the CS and US be repeatedly paired in a relatively fixed temporal relationship. Continuing our analogy, what are putative CSs in adaptation? One candidate CS is the visual target that cues an action. For example, in reaching studies, the CS could simply be the appearance of a visual target (Welch and Abel, 1970), particularly when the target onset not only provides information required to plan the reach (i.e., direction and extent), but also serves as an imperative for movement initiation. Typical experimental designs thus create a tight temporal link between a neutral sensory cue (the target) and movement, echoing the CS-US temporal constraints essential for eyeblink conditioning (Schneiderman and Gormezano, 1964).

Some adaptation studies have revealed so-called context-dependent effects, which can be viewed as conceptually similar to classical conditioning. For instance, when participants are presented with two opposing perturbations applied to the same movement path across interleaved trials, they exhibit marked interference, failing to compensate for either perturbation (Karniel and Mussa-Ivaldi, 2002; Wainscott et al., 2005). However, this interference can be attenuated if the opposing perturbations are associated with distinct contextual cues (Addou et al., 2011; Gandolfo et al., 1996; Hirashima and Nozaki, 2012; Hwang et al., 2006; Osu et al., 2004). Dynamic cues,

especially those that are task-relevant, such as varying the path of the early and late phases of movement, are especially effective in reducing this interference (Howard et al., 2013, 2015; Sheahan et al., 2016). Moreover, the temporal relationship between the cue and subsequent movement is critical: When a contextual cue precedes the movement by more than 600 ms, the interference between conflicting perturbations persists (Howard et al., 2012). Less clear is the efficacy of arbitrary, static sensory stimuli, such as color cues (Howard et al., 2012), although studies attempting to modulate adaptation with static cues have generally not imposed the strict temporal constraints required for context-dependent adaptation. The importance of temporal specificity is clearly reminiscent of eyeblink conditioning, where static cues (e.g., tones and light flashes) are extremely effective CSs insofar as they conform to strict temporal requirements (Smith et al., 1969).

While contextual cueing studies can be viewed as providing a foundation for an associative learning model of implicit adaptation, these handful of studies leave open three key issues, two practical and one theoretical. First, contextual cues have the potential to introduce confounding effects from explicit strategies (Howard et al., 2013; McDougle et al., 2015; Schween et al., 2020), and thus their influence might not reflect a pure modulation of implicit adaptation. Second, as mentioned above, the effect of static (versus dynamic) contextual cues remains controversial, perhaps due to variations in temporal requirements of the task (Howard et al., 2012). This issue must be addressed to convincingly link classical conditioning and implicit adaptation, given that the former historically relies on static CSs.

Third, and most important, discussion of potential similarities between classical conditioning and sensorimotor adaptation have been largely descriptive, focused mostly on their shared dependency on the cerebellum (Popa et al., 2016). The contextual cueing studies described above relate to one exemplary conditioning paradigm – differential conditioning – where distinct CSs predict distinct outcomes. However, building a theoretical bridge between

sensorimotor adaptation and classical conditioning requires drawing on more subtle concepts from the associative learning literature. In particular, from a conditioning perspective, the associative strengths of different CSs are additive (Rescorla and Wagner, 1972). For example, in compound conditioning, if two different CSs are simultaneously paired with a US, the associative strength of the compound stimulus is equal to the sum of the associative strength of each individual CS, which compete with one another. Fundamental conditioning principles like CS additivity (or competition) have ample support in behavioral and neural studies of associative learning, but have not, to our knowledge, been tested in the context of sensorimotor adaptation.

Here, we address these issues and examine the plausibility of an associative learning framework for understanding implicit sensorimotor adaptation. We measured and computationally modeled the effect of predictive CSs on trial-by-trial modulation of movements during adaptation. We employed a method that strictly isolates implicit adaptation and is readily amenable to presenting static CSs with precise temporal constraints. In Experiment 1, we verified differential conditioning effects under these conditions. In Experiment 2, we used a compound conditioning design to reveal that the conditioning principle of CS additivity applies to implicit sensorimotor adaptation. Together, our behavioral and modeling results provide evidence for a unifying framework for cerebellar-dependent learning, and may offer a parsimonious account of implicit sensorimotor adaptation.

RESULTS

In two experiments, we modified a visuomotor adaptation task to ask if learning would show two foundational classical conditioning phenomena, differential conditioning and compound conditioning. We opted to use clamped visual feedback, a technique that excludes strategic contributions and thus restricts learning to implicit motor adaptation (Morehead et al., 2017). With this method, the participant makes a rapid reaching movement to a visual target and is presented with a feedback cursor that follows a fixed ("clamped") path. On error trials, the cursor trajectory is rotated by an invariant angle from the target, regardless of the movement direction of the hand. On error-free trials, the cursor trajectory goes directly to the target. Participants are fully aware of the clamp manipulation and instructed to reach straight to the target on all trials attempting to ignore the task-irrelevant cursor. Critically, when presented with the deviated trajectory repeatedly over trials, the participant's reach angle gradually shifts in the direction opposite the clamp (Fig. 1A), and their behavior shows the cardinal signatures of implicit motor adaptation (Morehead et al., 2017; Kim et al., 2018, 2019; Parvin et al., 2018; Avraham et al., 2020; Tsay et al., 2020).

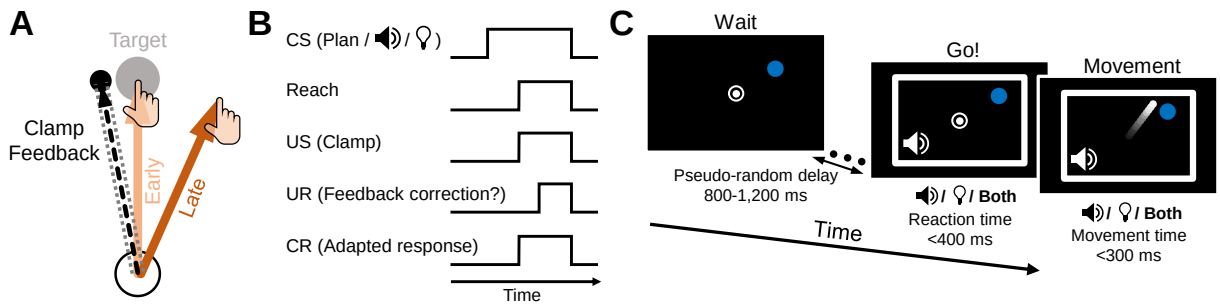

Figure 1. Reaching Task. (A) Clamped-feedback induces implicit adaptation. (B) Adaptation described as a conditioning process. (C) Participants reach to a single target (blue dot), moving a cursor (white dot) from a start location (white circle). The target is displayed in a fixed location for the entire experiment (location varied across participants), and the direction of the cursor trajectory is fixed ("clamped") on all trials. After a random delay, a tone and/or a light (white frame) is presented, serving as the movement imperative. This cue persists for the duration of the movement.

In the present experiments, we modified the clamp procedure by introducing manipulations borrowed from classical conditioning studies (Fig. 1B). We consider the clamped feedback as an unconditioned stimulus (US), timed instantaneously with the reach. The movement plan can be viewed as one conditioning stimulus (CS; Hirashima and Nozaki, 2012; Sheahan et al., 2016). Repeated pairing of this plan-based CS with the clamped feedback (US) forms an association that causes an adaptive conditioned response (CR) whenever the movement plan is elicited, even when visual feedback is absent. The movement plan is present on all reaching trials as it is fundamental to volitional movement. In most adaptation studies, the onset of the target cues the movement plan and serves as the imperative, making the target appearance a salient task-relevant stimulus. To eliminate this confound, a single target location was used in the current study and the target was visible throughout the entire task (Fig. 1C).

Critically, we tested predictions of classical conditioning using arbitrary sensory CSs: Drawing on classic work in animal learning (Pavlov, 1927; Rescorla and Wagner, 1972), we accomplished this by presenting sensory events (i.e., a tone or light) as the imperative cues for movement initiation (Fig. 1C). We thus created a situation where there were two putative CSs, one consisting of the movement plan directed at the target location (presumably with a strong preconditioned association with the task goal, i.e., visual feedback contacting the target), and one serving as the movement imperative (tone/light, which are neutral with respect to the task goal). The use of a neutral sensory stimulus to cue movement initiation provides a means to establish a tight temporal link between the light or tone and the US (clamp feedback), a prerequisite for cerebellar-dependent delay conditioning (Schneiderman and Gormezano, 1964). If the participant did not move within 400 ms of the imperative, a warning was given, reminding them to initiate the movement faster (Howard et al., 2012). Participants were able to comply with this requirement, exhibiting rapid reaction times (Mean±STD: 287±45.2 ms).

In terms of conditioning, feedback corrections elicited by a deviated clamp could constitute the unconditioned responses (UR). However, our primary goal here was to test the link between feedforward adaptation and classical conditioning. As such, we opted to focus on trial-to-trial changes resulting from adaptation. To this end, we required the participant to make rapid movements, “shooting” through the target. If movement time was longer than 300 ms, the participant was requested to move faster via an onscreen message. The conditioned response (CR) was operationalized as changes across trials in feedforward movement commands.

In differential conditioning, one CS is paired with the US (CS+) and another CS is presented without the US (CS-). Differential conditioning refers to the fact that only the CS+ should become associated with the US and result in a CR. We implemented this in Experiment 1 (Fig. 2A) by pairing one imperative cue (e.g., the tone) with a 15° error clamp to create a CS+ (i.e., prediction error present), and the other imperative cue (e.g., the light) with a 0° clamp to create a CS- (no prediction error). During the acquisition phase, CS+ and CS- trials, paired with their associated US+/US-, were randomly interleaved (Fig. 2B). This phase was followed by a probe phase in which CS+ and CS- trials were randomly presented in the absence of any visual feedback (no US).

Participants exhibited a marked change in movement direction during the acquisition phase, reaching an asymptote of ~15° (Fig. 2C). This rapid adaptation is consistent with previous adaptation studies, particularly those in which a single target always appears at the same location (Bond and Taylor, 2015; Day et al., 2016; McDougle et al., 2015, 2017).

The main analysis centered on the trial-by-trial changes in hand angle, with these data used to compare two canonical models of motor learning. The internal model framework was represented by the standard state-space model, a linear dynamical system model that captures the time course of learning in motor adaptation tasks (Eq. 1, see Methods). The classical conditioning framework was represented by the Rescorla-Wagner model, a model that formalizes

changes in conditioned responses via modulations in the associative strength of conditioned (and unconditioned) stimuli (Eqs. 2-4). For each model, we generated predictions using a fixed set of parameters (Fig. 2D). The state-space model predicts that the hand angle would be dictated by the state of the internal model that is updated based on the error experienced in the previous trial (trial *n-1*); we refer to this as the "adaptation effect." Critically, in this model, the hand angle would not be influenced by the current CS (trial *n*). In contrast, the Rescorla-Wagner model predicts that the two CSs would have different associative strengths in relation to the US, and as such, elicit different CRs on trial *n* ("Pavlovian effect") in addition to the adaptation effect of the CS experienced on trial *n-1*.

Consistent with the predictions of both models, a robust adaptation effect was observed (Fig. 2E, left panel): Trial-by-trial changes in reaching direction (Δ hand angle) were significantly affected by the CS presented on the previous trial [$F(1,15)=13.3$, $p=0.002$], such that the change in hand angle was larger after CS+ trials compared to after CS- trials. That is, the error occurring on CS+ trials (US+) resulted in learning that carried over to the next trial, whereas the absence of an error on a previous CS- trial (US-) resulted in a relative reversion to baseline (extinction).

The critical test of our hypothesis centers on within-trial, or "Pavlovian" effects. That is, will the reach angle on trial *n* be affected by whether the imperative is the CS+ or the CS-? The results revealed clear Pavlovian effects (Fig, 2E, both panels): The hand angle increased in the direction of adaptation on CS+ trials (i.e., a positive change in hand angle relative to previous trials) and decreased on CS- trials [$F(1,15)=5.83$, $p=0.029$]. This effect is consistent with classical conditioning, and accords with previous studies of contextual cueing (Hirashima and Nozaki, 2012; Howard et al., 2012, 2015; Sheahan et al., 2016). We also observed an interaction between CS identity on trials *n-1* and *n* [$F(1,15)=7.11$, $p=0.018$]. That is, the difference between CS+ and CS- was larger on trials following a CS- (Mean±SE, 1.09°±0.39°) compared to trials following a CS+ (0.65°±0.35°). This interaction effect may reflect an asymmetry between the rate of the

acquisition and extinction processes once the CS-US associations are established. That is, the state (or associative strength) following a CS+ trial may be closer to its asymptotic limit than after a CS- trial, and is thus more limited in its potential for further change.

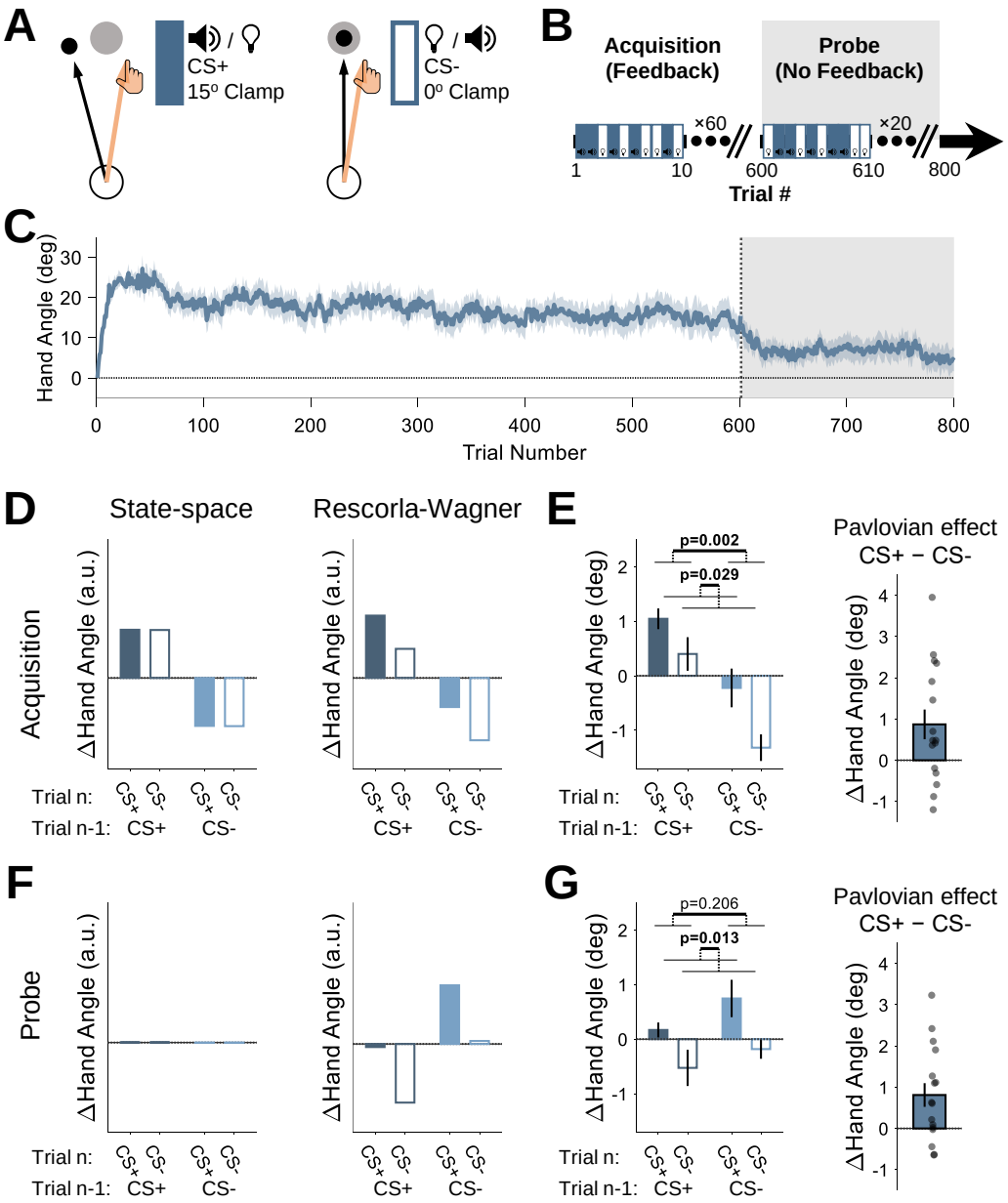

Figure 2. Experiment 1: Differential Conditioning. (A) Trial types. A 15° clamp (CW/CCW, counterbalanced across participants) was associated with CS+ and a 0° clamp with CS- (counterbalancing

the associations with the tone and light across participants). (B) Experimental protocol. CS+ (e.g., tone) and CS- (e.g. light) trials were randomly interleaved. Clamped feedback (±15°/0°) was presented during the acquisition phase (white background), and no feedback was provided during the probe phase (gray). (C) Mean hand angle time course (N=16). (D) Simulation results for trial-by-trial change (Δ) in hand angle during acquisition. While the state-space model predicts only an adaptation effect (main effect of trial *n-1*, dark vs light blue), the Rescorla-Wagner model also predicts a Pavlovian effect (main effect of the presented CS on the current trial *n*, filled vs empty bars). (E) Experimental results for trial-by-trial Δ hand angle during acquisition comport with the Rescorla-Wagner model simulations but not the state-space model simulations (left panel). The black outlined bar (right panel) presents the Pavlovian effect, i.e. the subtraction of hand angle changes between CS+ and CS- trials. (F, G) Similar to (D) and (E), respectively, but for the probe phase, showing a significant Pavlovian effect that is consistent with the Rescorla-Wagner model. Shaded regions and error bars represent SEM. Dots represent individual participants.

We note that the feedback was different on CS+ and CS- trials, with the cursor deviating from the target in the former and moving in a straight line to the target in the latter. This raises the possibility that the hand angle differences on CS+ and CS- trials could be affected by rapid feedback responses to the error. This explanation is unlikely given that the movements were quite rapid (Mean±STD, 103±31.2 ms). Moreover, when we directly computed feedback corrections (operationalized as the difference between the hand angle 50 ms after movement initiation and at the radial distance of the target), we observed no overall change in hand angle between the time points (Mean±STD, -0.32°±2.92°), and no significant difference between CS+ and CS- trials [$t(15)=-0.47$, $p=0.640$].

The probe phase, where the visual feedback is eliminated, provides a more stringent test for associative learning (Fig. 2F). Critically, here too we observed significant Pavlovian effects: Although there was an overall decrease in hand angle across the probe phase (i.e., a partial washout of adaptation, Fig. 2C), there was a significant main effect of the CS presented on trial *n* [$F(1,15)=7.98$, $p=0.013$] (Fig. 2G), with a relative trial-by-trial increase in hand angle on CS+ trials, and a relative trial-by-trial decrease on CS- trials. Moreover, there was neither effect of the *n-1*

CS [F(1,15)=1.74, p=0.206] nor an *n-1* x *n* interaction [F(1,15)=0.25, p=0.621], consistent with the expectation that trial-by-trial adaptation effects are abolished in the absence of error feedback.

The simulations shown in Figures 2D and 2F illustrate the basic predictions of each model, with parameter values chosen to approximate the mean experimental results. Crucially, the construction of the standard state-space model offers no potential parameter combination that can account for the observed behavior (Fig. S1). In contrast, differential conditioning effects of the CS+ versus CS- hold for virtually any combination of Rescorla-Wagner model parameters (Fig. S1).

Two additional analyses provide further support for the conditioning account over the internal model account. First, a direct model comparison favored the Rescorla-Wagner model over the state-space model (Fig. S2; *t*-test comparing sum of squared residuals, t(15)=-3.36, p=0.004; *t*-test comparing Akaike Information Criterion (AIC) values, t(15)=-5.60, p<0.001). Second, an *a posteriori* analysis tested a subtle but important aspect of our conditioning hypothesis: Given the putative low associative salience, and, consequently, lower learning rates (Eq. 4) for the neutral sensory imperative cues in our model, the contribution of these cues to the CR should initially be rather modest and gradually increase over time. Because these cues deterministically appear on different trial types, we can isolate their effects from the other putative CS, the movement plan (which appears on all trials, and is thus mainly realized in cumulative learning effects). That is, we can isolate the Pavlovian effect from the adaptation effect. We investigated the time-course of these dissociable effects by performing a trial-by-trial multiple regression analysis on the hand angle data (divided into 50-trial epochs), using the identity of the previous (*n*-1) and current (*n*) CS as two separable predictor variables competing for variance. Results of this analysis supported the conditioning model: As shown in Figure S3, the Pavlovian effect related to the (trial *n*) imperative cues emerged gradually during acquisition, whereas the

adaptation effect (i.e., trial *n-1*) was much larger, emerged quickly, and then stabilized. Rescorla-Wagner model simulations echoed this result.

Importantly, the observed Pavlovian effects did not appear to be affected by awareness of the CS-US contingency. Participants that correctly identified the pattern of associations between the imperatives and the type of feedback in a post-experiment survey ("aware" sub-group) did not exhibit a different Pavlovian effect than an "unaware" sub-group, in either the acquisition ($t(14)=-0.333$, $p=0.744$, $BF_{10}=0.446$) or probe ($t(14)=-0.081$, $p=0.937$, $BF_{10}=0.431$) phases. This finding is consistent with work on human delay eyeblink conditioning, which was also found to proceed outside of awareness (Clark and Squire, 1998).

In summary, the results from both the acquisition and probe phases in Experiment 1 are consistent with predictions derived from an associative learning. Feedforward implicit motor adaptation – here operationalized as the CR – was differentially modulated by the CS+ and CS-, with a greater response to the CS+, the cue paired with a visuomotor error.

In Experiment 2, we put the associative learning account through a more stringent test. We used a compound conditioning design to investigate a fundamental tenet of the Rescorla-Wagner model, where the strength of the CR reflects the sum of the associative effects of all presented CSs (Eq. 2; Rescorla and Wagner, 1972). In compound conditioning, two or more sensory stimuli form a compound CS by being presented simultaneously. When paired with a US, this compound CS comes to elicit CRs. Critically, each element of the compound, when presented alone, elicits a proportionally weaker CR, with the degree of attenuation being a function of the associative strength of that CS.

During the acquisition phase of Experiment 2 we presented a 15° error clamp stimulus on all trials, and paired it with a compound CS (i.e., the simultaneous presentation of the tone and

light; Fig. 3A, 3B). As in Experiment 1, we again observed robust adaptation in the acquisition phase, manifest as a rapid change in hand angle in the direction opposite to the clamp (Fig. 3C).

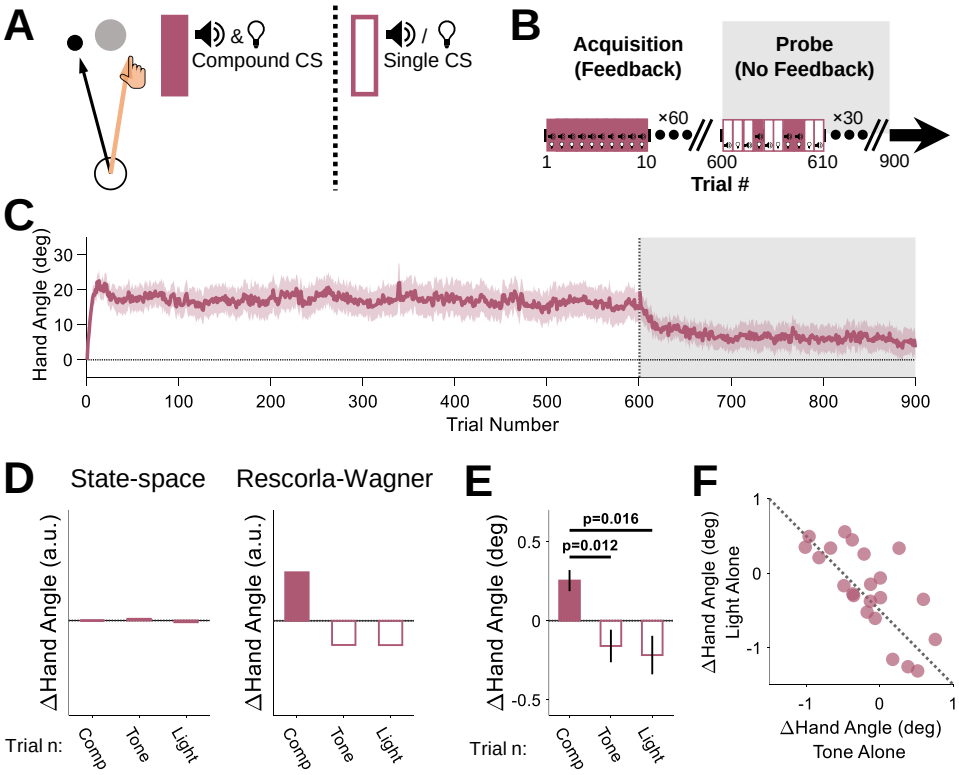

Figure 3. Experiment 2: Compound Conditioning. (A, B) During acquisition, a 15° clamp was associated with a compound CS: Tone and light were presented simultaneously as movement imperatives. During the probe phase, no feedback was provided, and the CSs were presented either together (Compound CS) or alone (Single CS; tone or light). (C) Mean hand angle time course (N=22). (D) Simulation results for trial-by-trial Δ hand angle during the probe phase for the compound CS (filled bar) and each of its elements (empty bars). Unlike the state-space model, the Rescorla-Wagner model predicts a positive relative change for the compound CS on the current trial *n* and a negative relative change for each element. (E) Experimental results for the Δ hand angle during the probe are in line with the Rescorla-Wagner model. (F) Scatter plot showing the relationship between individuals' responses to the elemental CSs (the dotted black line represents the unity line). Shaded regions and error bars represent SEM. Dots represent individual participants.

Acquisition was followed by a probe phase in which the clamp feedback was eliminated (Fig. 3B). The imperative in the probe phase could now be either the same compound CS used during the acquisition phase, or a singleton cue presented alone (i.e., either the tone or light). We observed a significant Pavlovian effect of CS type in the participants' movements on these trials [$F(2,42)=4.78$, $p=0.014$], with larger hand angles on compound CS trials versus both the tone-alone or light-alone trials (Fig. 3E). These results are again consistent with the Rescorla-Wagner model but cannot be explained by the standard state-space model (Fig. 3D).

The additivity (or cue competition) principle in classical conditioning also states that there should be a negative correlation between the associative strengths of competing CSs (Rescorla and Wagner, 1972). That is, if a strong associative bond is formed between one CS and the US, this will come at the expense of the associative strength accrued by any competing CSs (Eq. 2). This pattern was indeed observed when comparing responses to the tone-alone and light-alone trials: Participants showing a large trial-by-trial increase in hand angle for the tone tended to exhibit a relative decrease in hand angle for the light, and vice versa (Fig. 3F, Pearson correlation: $r=-0.72$, $p<0.001$). This striking correlation reflects competition between the elements of the compound CS, a key prediction of the Rescorla-Wagner model.

To this point, our analyses of the compound conditioning results have focused on the responses to the CS on trial *n*, regardless of the CS identity on the previous trial. However, as observed in the results of Experiment 1 with differential conditioning, even in the probe phase where the visual feedback is eliminated (Fig. 2G), the trial-by-trial change in hand angle was influenced not only by the CS on trial *n*, but also by the CS on trial *n-1*. Thus, to examine the distinct response of the compound CS with respect to its elements, while also accounting for the behavior on the previous trial, we pooled the two elemental CSs of the compound (the singletons conditions) into a single CS-alone condition. Then we examined the effects of the previous and current CS type (single versus compound) on the observed change in hand angle. We again

observed the predicted Pavlovian effect [$F(1,21)=21.2$, $p<0.001$]: There was a marked relative increase in hand angle for the compound CS (Mean±SE, 0.24°±0.06°) and a relative decrease for the single CS (-0.18°±0.06°). There was neither significant main effect of the CS on trial *n-1* [$F(1,21)=0.012$, $p=0.915$] nor any trial *n-1* × trial *n* interaction [$F(1,21)=0.276$, $p=0.605$], likely due to the absence of visual feedback having eliminated trial-by-trial adaptation.

DISCUSSION

Sensorimotor adaptation and eyeblink conditioning have provided foundational paradigms for the study of motor learning, yielding key insights for theoretical and neural models of learning and memory, particularly with respect to cerebellar function. A control engineering perspective has generally been applied to modeling sensorimotor adaptation (Krakauer et al., 2019; Shadmehr and Krakauer, 2008; Wolpert and Flanagan, 2001), advancing the notion that changes in behavior arise from simulations of internal models of motor commands to anticipate their consequences. In contrast, eyeblink conditioning has been described as a model-free associative learning process. Our motivation in this work was the desire to bring together these two diverging literatures, and to highlight similar behavioral effects and overlapping neural mechanisms. Inspired by parsimonious models of classical conditioning (Rescorla and Wagner, 1972), we sought to reconsider adaptation as a manifestation of associative learning.

To this end, we tested if, and how, behavioral changes observed in sensorimotor adaptation can be captured by fundamental computational principles of classical conditioning, specifically, associability (Experiment 1) and additivity (Experiment 2). Our results provide the first evidence that, when properly timed, neutral and static sensory stimuli (CSs) paired with distinct visuomotor outcomes can differentially influence feedforward adaptation of reaching movements. In addition, we discovered that associating a visuomotor error with a compound CS resulted in a higher adaptive response to the compound than to each of its two elements, and observed a striking between-participant anti-correlation between the adaptive responses to these elements, comporting with the additivity principle put forth by Rescorla and Wagner (1972). Our results cannot be captured by the typical state-space model of adaptation, regardless of how it is parameterized (Fig. S1); however, they are clearly consistent with the Rescorla-Wagner model (Figs. 2 and 3). We believe these findings go beyond superficial links between adaptation and eyeblink conditioning. Rather, we believe they constitute a first step in the development of a more

cohesive algorithmic framework for understanding cerebellar learning across widely different tasks.

The predominant model of motor adaptation states that adaptation is driven by the updating of an internal forward model. A core function of the forward model is to simulate predicted sensory consequences of descending motor commands, providing a representation that can be compared with the observed outcomes, with any discrepancy between these quantities being used to update the internal model (Wolpert et al., 1995). This framework is well-suited for a control system hampered by the transmission delays inherent in an embodied agent. However, a number of lines of evidence have highlighted how implicit adaptation, when isolated from other learning processes, is a curiously stereotyped learning system that can even, given certain experimental constraints, produce outputs that are counterproductive to performance (Mazzoni and Krakauer, 2006; Morehead et al., 2017). For example, participant's initial response to a mirror reversal visual perturbation is in the opposite direction to the optimal solution, as if the visual feedback is rotated (Wilterson and Taylor, 2020). These observations have motivated recent efforts to reframe sensorimotor adaptation as the result of more rigid "direct policy updating" rather than the updating of a flexible forward model (Hadjiosif et al., 2020). Here, we offer a novel account that is compatible with a putative direct policy update, one that does not require any model-based internal simulation – associative learning, with a strong prior to adapt movements in the direction opposite to the observed errors.

An attempt to find consilience between associative learning processes like classical conditioning of eyeblinks and other cerebellar-dependent learning tasks is not without precedence. For instance, Raymond et al. (1996) made the conjecture that adaptation of the vestibulo-ocular reflex (VOR) could be reframed as a conditioning process, with the error signal given by experimentally-induced image motion on the retina acting as a US, and the vestibular stimulus, driven by a head turn, acting as a conditioning stimulus (CS) (Raymond et al., 1996).

Moreover, several studies of human motor adaptation to force-field perturbations have demonstrated that certain movement-related contextual cues can help form separate motor memories during adaptation in a manner consistent with classical conditioning (Addou et al., 2011; Hirashima and Nozaki, 2012; Howard et al., 2012, 2013, 2015; Osu et al., 2004; Sheahan et al., 2016). However, to our knowledge, no study to date has directly tested fundamental computational principles of classical conditioning in the context of visuomotor adaptation, while simultaneously isolating implicit learning.

In our effort to frame adaptation as a form of conditioning, it is important to note that the former has various features that are absent in the latter. First, adaptation is sensitive to the sign of the error; in visuomotor adaptation, this sensitivity is reflected in the gradual deviation of the movement direction opposite to the direction of the perceived error. At first blush, it is not clear that the error in most conditioning tasks, like eyeblink conditioning, is similarly signed. However, it is important to consider that the update of the CR is driven by a prediction error, which could be positive or negative with respect to the expected feedback (Albus, 1971). Moreover, both the cerebellar-dependent VOR and saccade adaptation processes are determined by the directional sign of a prediction error (Boyden et al., 2004; Kojima et al., 2004). Indeed, such directional tuning to errors has been observed in the cerebellum (Herzfeld et al., 2018; Kojima et al., 2010; Soetedjo et al., 2008), and likely extends to reaching errors.

Second, by definition, classical conditioning paradigms like eyeblink conditioning do not involve an instrumental component, while visuomotor adaptation tasks require volitional movement. In that sense, motor adaptation is perhaps more akin to operant than classical conditioning. While the elements of models for operant and classical conditioning are indeed different, and likely engage non-identical processes (Brembs and Plendl, 2008; Lorenzetti et al., 2006; Ostlund and Balleine, 2007), it is also clear that both can be viewed as outcomes of a CS-US association (Brembs and Heisenberg, 2000). Fundamentally, this distinction does not change

our account; concordantly, the underlying computational model we employed (Rescorla and Wagner, 1972) is applicable to both cases. Furthermore, the volitional movement plan, driven by the presentation of the visual target (or imperative cue), could be considered as a “pre-conditioned” CS, one that has a strong baseline association with the non-perturbed sensory feedback experienced in everyday movement.

The idea of a movement plan acting as a CS is supported by multiple lines of evidence. First, “follow-through” movements can serve as sufficient cues to allow seemingly identical pre-movements be associated with distinct perturbative errors (Sheahan et al., 2016). Even though the implementations of these follow-through movements are deferred until after errors have been experienced, it is presumably planned before the movement is made. This can be seen as a form of differential conditioning, with different motor plans serving as unique CSs. Furthermore, these high-level motor plans appear to maintain this associative quality even when they are simply imagined by the participant without being executed (Sheahan et al., 2018). Second, recent evidence suggests that the generalization function for implicit adaptation is yoked to participants’ explicit movement goals (Day et al., 2016; McDougle et al., 2017), reinforcing the notion that implicit adaptation is tied to the movement plan. Third, there is ample neurophysiological support for a top-down motor command behaving like a CS: Descending motor commands (efference copies) constitute a major source of input to the cerebellar cortex, and are associated with motor errors during learning (Blakemore et al., 2001; Gao et al., 2016; Kawato and Gomi, 1992; Khilkevich et al., 2018; Wolpert et al., 1998). Thus, our focus on associative learning fits with the conventional notion of the cerebellum as a high-throughput pattern recognition device (Marr, 1969), which is, arguably, an optimal substrate for representing a diverse set of associations.

We also note that considering the movement plan as akin to a CS implies that an internal representation links motor commands to predicted sensory consequences. As such, our account is broadly consistent with a conventional internal forward model. However, under the conditioning

framework, this representation is fully described as the outcome of a straightforward associative learning process (i.e., essentially a look-up table) without requiring any form of model-based forward simulation. Thus, while functionally related, the forward model framework and the associative learning framework are algorithmically and mechanistically distinct.

On a more speculative note, a parsimonious account of sensorimotor adaptation as associative learning could avoid one additional problem in the forward model account; namely, the computational cost one would expect to accompany a forward simulation process. Simulation-based accounts for movement planning and motor learning are perhaps better suited for describing top-down, cognitive behaviors, such as the strategic aiming of movements (Haith et al., 2015; McDougle and Taylor, 2019; Schween et al., 2020). Indeed, forward simulations are typically linked to high-level cognitive tasks that require planning, such as spatial navigation and multi-step decision-making (Doll et al., 2012). Moreover, the framing of implicit sensorimotor adaptation as an outcome of a model-based simulation process rather than a model-free associative learning process also echoes certain broader distinctions between control engineering and machine learning approaches. In the former, feedforward adaption could be assumed to reflect changes in a complex internal model, whereas in the latter, it can be described as the result of robust associations established through repeated training (e.g., via deep reinforcement learning; Heess et al., 2017).

Further work is certainly required to provide a more systematic investigation of the utility of associative learning models for understanding sensorimotor adaptation. First, as currently framed, we do not provide an analog of the unconditioned response (UR) in reach adaptation. Online feedback corrections could perhaps fill this gap: Rapid feedback corrections are comparable to reflexive eyeblinks in that they entail automatic responses to errors, evolving into feedforward (conditioned) responses over time (Albert and Shadmehr, 2016). Because we opted to use rapid shooting movements to isolate feedforward adaptation, no reliable feedback

corrections were observed. Importantly, specifying a UR is not a necessary precondition for characterizing a conditioning process; indeed, at the level of the UR, the line between classical and instrumental conditioning is blurred. For example, in Pavlovian-to-Instrumental transfer, a behavior learned through classical conditioning influences subsequent volitional behavior (Cartoni et al., 2016).

Another curiosity is the incomplete unlearning we observed in the no-feedback probe phase of both experiments, with reach angles remaining deviated in the direction of adaptation (Figs. 2C and 3C). Given the rapid pace of learning in the acquisition phase, these persistent aftereffects are not predicted by either the basic state-space model or the Rescorla-Wagner model. However, persistent aftereffects are not uncommon in adaptation tasks, and are especially robust when error feedback is simply removed rather than replaced by veridical feedback (Brennan and Smith, 2015), perhaps reflecting a use-dependent Hebbian form of learning (Verstynen and Sabes, 2011). The prolonged aftereffects we observed in the probe phase could, in theory, be captured by state-space models that contain two parallel learning components, such as separate fast and slow learning states (Smith et al., 2006). While multi-rate state-space model may be able to capture the overall shape of the acquisition and extinction functions, they would still fail to explain the differential and compound Pavlovian effects we observed. Future studies using more complex tasks designed to dissociate multiple learning components could be used to expand the conditioning account to accommodate a two-state learning model and additional use-dependent effects.

Lastly, we caution that our findings do not directly refute nor falsify conventional explanations of adaptation, such as the forward model, nor do they speak to the utility of such models in explaining other types of motor behaviors. The results do suggest that, at the very least, associative learning processes may be superimposed onto model-based adaptation. However, if an associative learning account can successfully explain various forms of cerebellar motor

learning, we believe parsimony should favor it over a forward model-based account. Moreover, the associative learning framework is supported by decades of conditioning literature; thus, the proposal is rooted in well-known psychological and neurophysiological mechanisms.

METHODS

Participants

Thirty-eight healthy volunteers (aged 18-31 years; 31 females) participated in one of two experiments, 16 participants in Experiment 1 and 22 in Experiment 2. All participants were right-handed, as verified with the Edinburgh Handedness Inventory. The protocol was approved by the Institutional Review Board at the University of California, Berkeley.

Experimental setup and task

The participant sat at a custom-made table that housed a horizontally mounted LCD screen (53.2 cm by 30 cm, ASUS), positioned 27 cm above a digitizing tablet (49.3 cm by 32.7 cm, Intuos 4XL; Wacom, Vancouver, WA). The participant held in their right hand a hockey paddle that contained an embedded digitizing stylus. The monitor occluded direct vision of the hand, and the room lights were extinguished to minimize peripheral vision of the arm. Reaching movements were performed by sliding the paddle across the tablet. The sampling rate of the tablet was 200 Hz. The experimental software was custom written in Matlab (The MathWorks, Natick, MA), using the Psychtoolbox package (Brainard, 1997).

At the beginning of each trial, a white circle (0.5 cm diameter) appeared at the center of the black screen, indicating the start location (Fig. 1C). The participant moved the stylus to the start location. Feedback of hand position (i.e., the stylus position) was indicated by a white cursor (0.3 cm diameter), only provided when the hand was within 1 cm of the start location. A single blue target (0.5 cm diameter) was positioned 8 cm from the start location. In the classical conditioning framework, the target, which also drives the movement plan, should constitute a very salient CS if it is presented in temporal contingency with the US, the visual feedback associated with the movement (see below). To eliminate this temporal contingency, the target remained

visible at the same location during the entire experiment. For each participant, the target was placed at one of four locations, either 45°, 135°, 225°, and 315°, and this location was counterbalanced across participants.

Movement initiation was cued by the presentation of the neutral (non-spatial) CS(s). We used two different CSs, a tone and a light, which are both assumed to have no inherent association with the US. The tone CS was a pure sine wave tone with a frequency of 440 Hz. The light CS was a white rectangular frame [39.4 cm X 26.2 cm] that spanned the perimeter of the visual workspace. The large frame was selected to provide a salient visual stimulus, but one that would not be confused with the target. The CSs appeared following a pseudo-random and predetermined delay from the time the cursor was in the start location. The delay ranged between 800-1,200 ms (in steps of 100 ms), and was drawn from a uniform distribution.

Depending on the specific experimental protocol and task phase, the CSs could appear alone or together on a trial. The onset of the CS served as the imperative signal, with the participant instructed to rapidly reach directly towards the target upon perceiving the imperative, slicing through the target. The CS was terminated when the hand reached 8 cm, the radial distance to the target (Fig. 1C). To minimize the delay between the onset of the CS and the US (the error clamp), the auditory message “start faster” was played whenever the reaction time (RT) exceeded 400 ms. RT was operationalized as the interval between CS onset and the time required for the radial distance of the hand to exceed 1 cm. To encourage rapid movements, the auditory message “move faster” was played when the movement time exceeded 300 ms, with the end of the movement operationalized as the point where the radial distance of the hand reached 8 cm.

For the unconditioned stimulus (US), we used task-irrelevant clamped feedback (Morehead et al., 2017). With clamped feedback, the radial position of the visual cursor is matched to the radial position of the hand. However, the angular position of the cursor is fixed. The participant thus controlled the speed and radial distance of the cursor, but not its direction. When

designed to produce a prediction error and elicit implicit sensorimotor adaptation, the clamp followed a path that deviated from the target by 15°, with the direction, i.e., clockwise (CW) or counterclockwise (CCW), counterbalanced across participants. We also included no-error trials (Experiment 1) by presenting a clamped feedback that followed a path directly to the target (0° clamp; Fig. 2A). The nature of the clamp manipulation was described in detail to the participant, and they were explicitly instructed strictly to ignore the feedback, aiming their reach directly toward the target on every trial. These instructions were designed to emphasize that the participant did not control the cursor position, and that they should always attempt to reach directly to the target. The instructions of the task were reinforced by the presentation of short video animations to demonstrate how the CSs would serve as imperative signals, as well as to show the invariant direction of the clamped feedback.

Experimental protocol

Both Experiments 1 and 2 included two phases: acquisition and probe. During the acquisition phase, clamped feedback was presented on each trial, serving as the US. During the probe phase, the clamped feedback was not presented. In both phases, the participants were instructed to reach straight to the target as soon as the imperative CS appeared. Note that we opted to not include baseline reaching blocks prior to the start of the acquisition phases to avoid introducing any incidental associations between the target, movement plan, and any other contextual variables. A ~1 minute break was provided in the middle of the experiment.

<u>Experiment 1: Differential conditioning</u>

Experiment 1 (N=16) was designed to test differential conditioning in the context of a sensorimotor adaptation task. The session consisted of 800 trials: 600 acquisition trials followed by 200 probe trials (Fig. 2A, 2B). One of two CSs (tone or light) was presented on each trial, serving as the

imperative for the reaching response. During the acquisition phase, one CS was paired with a 15° clamped error feedback (CS+ condition) and the other CS was paired with a 0° clamped feedback (CS- condition). Each CS was presented on 50% of the trials, and the assignment of the tone and light to the CS+ and CS- was counterbalanced across participants. During the probe phase, each CS was presented alone on half of the trials, and there was no visual feedback. For both the acquisition and probe phases, the CS+ and CS- trials were interleaved in a pseudo-random order that was unique to each participant. To ensure that the participant would not be able to predict the CS type, the generated trial sequence for each participant was assessed to verify that there was no significant lag-1 autocorrelation in the time series. At the end of the experimental session, we assessed whether participants were aware of the contingency between each CS and its associated feedback, asking, “did you identify any pattern in the experiment?” in a free-response survey.

Experiment 2: Compound conditioning

The adaptation task was modified in Experiment 2 (N=22) to provide a test of compound conditioning. The procedure was mostly the same as that used in Experiment 1, with the following changes. First, the session consisted of 600 acquisition trials and 300 probe trials (Fig. 3A,3B). Second, a compound CS, consisting of both the tone and light, served as the imperative throughout the acquisition phase. Moreover, the compound CS was always paired with 15° clamped feedback. Lastly, the probe phase, in which the visual feedback was removed, consisted of 100 trials each of the compound CS, tone alone CS, and light alone CS.

Model simulations

Trial-by-trial reach angles were simulated using two canonical learning models: the state-space model and the Rescorla-Wagner model. The former was employed to represent the internal model

framework, and the latter to represent the classical conditioning framework. To illustrate the predictions of the models, we used a single set of fixed parameters for each model in all simulations (Figs. 2D, 2F, 3D). For the Rescorla-Wagner model, we chose parameters that result in qualitatively similar effects to the experimental results. No such parameters exist for the state-space model. To demonstrate that the conditioning effects predicted by the Rescorla-Wagner model are qualitatively independent of the particular parameters used in the simulations, and that they cannot be captured by the state-space model, we also simulated behavior over a wide range of parameter values to generate various predicted effect sizes (Fig. S1, see details below).

In the standard state-space model of motor adaptation, the state of the internal model (*x*) is updated according to the learning rule:

$$x_{n+1} = Ax_n + Be_n \quad (1)$$

where *e* is the sensory prediction error experienced on trial *n*, *A* is the retention factor, and *B* is the learning rate. With clamped feedback, the sensory prediction error is fixed to one of two values during the acquisition phase, either -15° on CS+ trials or 0° on CS- trials. The sensory prediction error is set to 0° on all trials in the probe phase. For the simulations presented in Figures 2D, 2F and 3D, we set the *A* to a value of 0.9 and *B* to 0.15.

As an alternative to the state-space model, the learning function during adaptation can be described with a variant of the Rescorla-Wagner model. Here, the associative strengths, *V*, of the conditioning stimuli are updated according to the following equations:

$$V(S)_n = \sum_{i=1}^{nS} V(s)_i \quad (2)$$

$$\partial(s)_n = \alpha(s) \cdot (\lambda - V(S)_n) \quad (3)$$

$$V(s)_{n+1} = V(s)_n + \beta\partial(s)_n \quad (4)$$

$V(S)$ in Equation 2 represents the sum of associative strengths for each individual conditioning stimulus $V(s)$ over the number of stimuli nS presented on trial n. The value of ∂ reflects the prediction error (Eq. 3), which is dependent on the salience of stimulus s, $\alpha(s)$, the asymptotic learning level for the US, λ, and the current total associative strength, $V(S)$. Equation 4 describes the update process for the associative strength of each stimulus s, where β represents the learning rate. Note that the summation in Equation 2 is used in the computation of the prediction error (Eq. 3), reflecting the additivity (or competition) principle.

In typical simulations of classical conditioning behaviors such as eyeblink conditioning, λ and V are normalized and the dependent variable is expressed as a percentage of trials in which a conditioned response occurs. However, the Rescorla-Wagner model can, in principle, compute any dependent variable (e.g., reaching angle). For all simulations, we set λ to 20° (similar to the observed implicit adaptation asymptotes in other studies, Bond and Taylor, 2015; Morehead et al., 2017; Kim et al., 2018, 2019), β to 0.2, and the three salience parameters (α's) for the movement plan CS, tone CS, and light CS, to, respectively, 0.6, 0.0009, and 0.0009. These divergent salience values reflect our assumption that most of the associative strength of the US would be absorbed by the movement plan CS, given its central relevance to the task goal of reaching to a target. The remainder of potential associative strength to the US is thus available for the tone and light CSs.

Although the two models yield many similar features of learning (e.g., sharing the Markov property, producing exponential-family learning curves, etc.), the additional parameters in the Rescorla-Wagner model allow it to capture the effects of differential and compound conditioning, should these processes be operative in our experiments. For example, in the differential conditioning case, modifying the parameters of the Rescorla-Wagner model could produce changes in the magnitude of both the within-trial "Pavlovian" effects (i.e., the modulation of behavior in response to the current CS presented, or "trial n" effects) and across-trial adaptation

effects (i.e., the modulation of behavior in response to the current state of learning, or "trial *n-1*" effects). However, the Rescorla-Wagner model will always yield unique responses to the CS+ and CS- given non-zero salience parameters. In contrast, no combination of the *A* and *B* parameters in the state-space model will produce differential responses to the tone and light CSs. To illustrate how the particular choice of parameters in the Rescorla-Wagner model influences the predicted conditioning effects, we simulated behavior using various combinations of the free parameters. We chose several combinations of values for β and λ, and, for each combination, a wide range of values for α_{Plan}, α_{tone} and α_{light}. (For simplicity, we constrained α_{tone} and α_{light} to the same value.) Figure S1 displays heatmaps resulting from these simulations, with the color of each cell corresponding to the simulated difference in the trial-by-trial change in hand angle between CS+ and CS- trials.

To simulate the dynamics of the adaptation and Pavlovian effects in differential conditioning (Fig. S3), and to compare it to the dynamics observed in the actual data, we simulated the hand angle during acquisition (600 trials) according to the Rescorla-Wagner model ($V(s)$ in Eqs. 2-4), based on the schedules of CS+ and CS- trials that were presented to the participants (16 simulated time courses). We then binned the simulated hand angle into epochs of 50 trials. For each bin, we performed the same trial-by-trial multiple regression analysis we performed on the actual data (Fig. S3, see *Data analysis* below). The simulated hand angle was the dependent variable, and the identity of the previous (*n*-1) and current (*n*) CS were separable predictor variables (z-scored) that, including an interaction term, competed for variance. Figure S3 presents the mean±SEM regression β weights of all simulated time courses for the previous (adaptation effect) and current (Pavlovian effect) predictors.

Model fitting and comparison

We conducted a *post-hoc* model comparison analysis (Fig. S2). In this analysis, we fit the standard state-space model (Eq. 1) and the Rescorla-Wagner model (Eqs. 2-4) to participants' hand angle time course data from Experiment 1. The two models were fit by minimizing the sum of squared residuals between the measured and modeled movement data, using the MATLAB function *fmincon*. To avoid local minima, 200 randomized sets of initial parameter values were used during fitting and the best fit of each model was selected for model comparison. Models were compared using both the sum of squared residuals and the Akaike Information Criterion approximated on the residuals (AIC; Akaike, 1974). All free parameters were bound at [0, 1], with the exception of λ, which was bounded at [0, 60]. We did not perform model fitting for Experiment 2 due to the fact that each trial was identical in the acquisition phase. As such, the salience parameters in the Rescorla-Wagner model for the light, tone, and plan are unidentifiable, and both models make indistinguishable behavioral predictions during acquisition.

Data analysis

The recorded position of the digitizing stylus was analyzed using custom-written MATLAB scripts. Our main analyses focused on the reach direction (hand angle) and, for learning, the trial-by-trial changes in hand angle (Δ hand angle). Hand angle was defined by two imaginary lines, one from the start position to the target and the other from the start position to the hand position at maximum movement velocity.

Trials in which the hand angle was larger than 100° off from the target, or in which the trial-to-trial change in hand angle was larger than 25°, were considered outliers and not included in the analyses. These outliers constituted 0.03% and 0.16% of all trials in Experiments 1 and 2, respectively. For the change in hand angle analysis, but not for the presentation of hand angle time courses, we excluded trials in which the reaction time exceeded 400 ms and/or movement

time exceeded 300 ms (Experiment 1: 11% of acquisition trials, 4.3% of probe trials; Experiment 2: 3.4% of acquisition trials, 4.9% of probe trials).

For all analyses and to visualize the results, the sign of the hand angle was flipped for participants who experienced a CCW clamp, such that a positive hand angle is in the direction of expected adaptation (i.e., opposite the direction of the perturbed feedback). Moreover, the hand angle on the first acquisition trial was treated as the baseline reaching angle and subtracted from the hand angle on all subsequent trials. (We note that the results remain unchanged in terms of statistical comparisons if this baseline subtraction step is omitted.)

In Experiment 1, the primary analyses examined how the Δ hand angle was influenced by the CS type (CS+ vs CS-), either in terms of the previous trial (*n-1*, adaptation effect) or current trial (*n*, Pavlovian effect). For each participant and phase, we calculated the average Δ hand angle for four types of trials: CS+ trials that follow CS+ trials, CS- after CS+, CS+ after CS-, and CS- after CS-. For each phase, a two-way repeated-measures ANOVA was conducted with two within-participant independent factors, the CS on trial *n-1* and the CS on trial *n*, each with two levels, CS+ and CS-. The Δ hand angle was the dependent variable in the two ANOVAs. To examine the dynamics of the adaptation and Pavlovian effects (Fig. S3), we did the same trial-by-trial regression analysis described above for the simulated hand angle (see Model simulations) with the exception that the dependent variable was now the actual hand angle data of each participant.

To assess whether the Pavlovian effect is influenced by the awareness about the contingency between each CS and its respective feedback, we divided the participants based on their responses to the post experiment questionnaire (see Experimental protocol): 7 out of the 16 participants stated the correct contingency between the CS and the visual feedback, and were thus considered the “aware sub-group.” The rest of the participants (N=9) reported that they did not identify any pattern related to the CS-US contingency and were considered the “unaware sub-group.” Independent two-sample *t* tests were used to compare the Pavlovian effects between

these groups during the acquisition and probe phases of the experiment. For these tests we also report Bayes factor BF_{10}, the ratio of the likelihood of the alternative hypothesis (H_1) over the null hypothesis (H_0) (Kass and Raftery, 1995).

Feedback correction was operationalized as the difference between the hand angle measured at the radial distance to the target and at 50 ms after movement initiation. We estimated the mean and standard deviation of feedback correction across all acquisition trials in all of the participants in Experiment 1. In addition, we calculated, for each participant, the mean feedback correction for each of the CS+ and CS- trials, and used a paired-sample *t* test to examine within-participant changes in feedback correction between the two trial types.

In Experiment 2, the analysis focused on the probe phase in which there was no visual feedback, comparing hand angles in response to the three imperatives (compound CS, light alone, tone alone). We compared the Δ hand angle to the three CSs on trial *n* regardless of the CS presented on trial *n-1*. We fit a one-way repeated-measures ANOVA, with the Δ hand angle as the dependent variable, and the CS type as the within-participant independent variable.

The additivity principle of the Rescorla-Wagner model states that the association strengths of each element of the compound CS will compete for associative strength with respect to the US (Eqs. 2-4). This principle was tested in our data by examining the correlation between the Δ hand angle associated with the tone and light CSs in Experiment 2.

SUPPLEMENTARY FIGURES

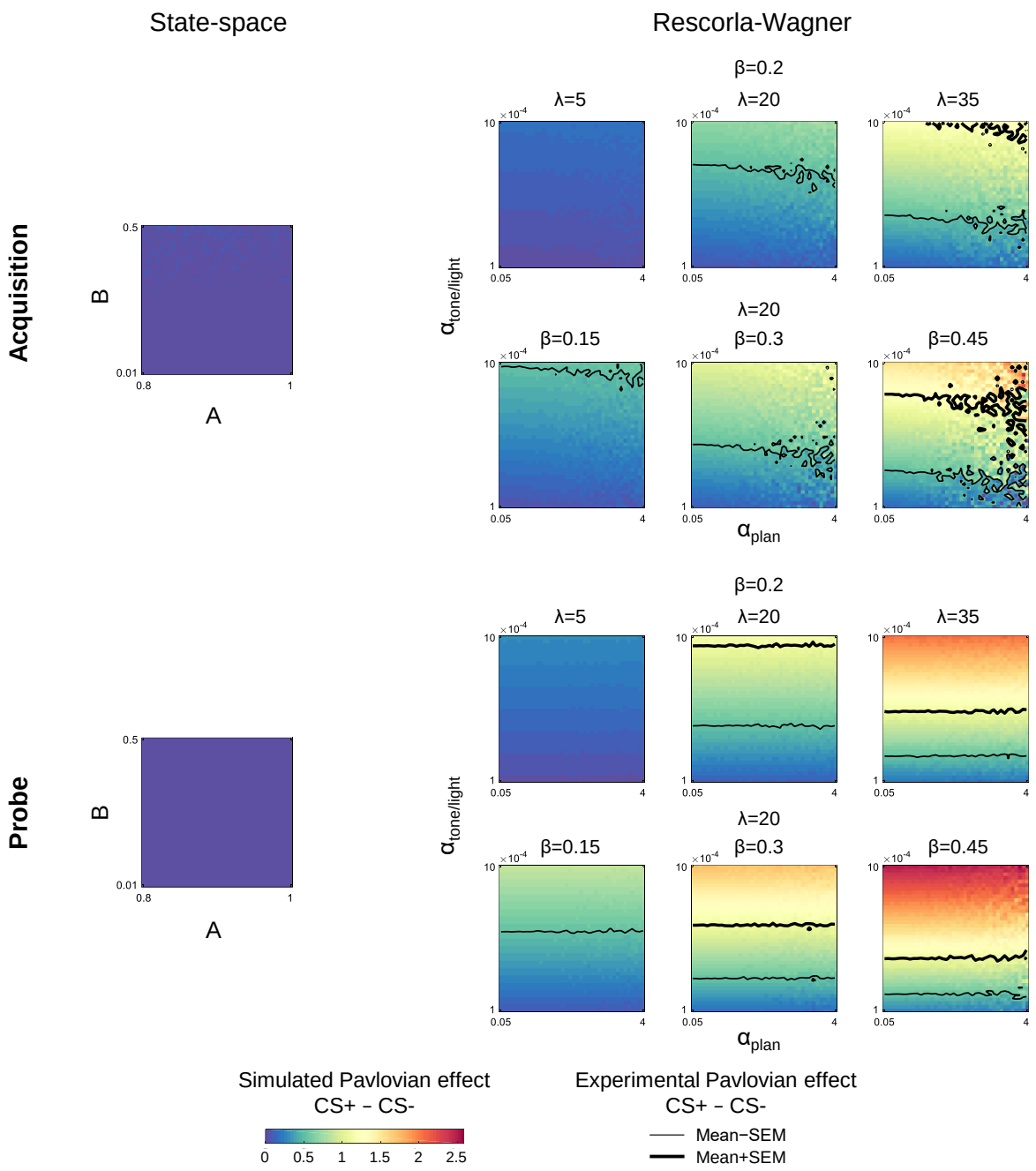

Figure S1. Simulations of Pavlovian effects in differential conditioning. Simulations of current trial CS effect, i.e. the difference between the change in hand angle on CS+ and CS- trials, for the acquisition (top panel) and probe (bottom panel) phases of Experiment 1, as predicted by the state-space (left) and Rescorla-Wagner (right) models. Contours represent mean±SEM of the Pavlovian effect from Experiment 1.

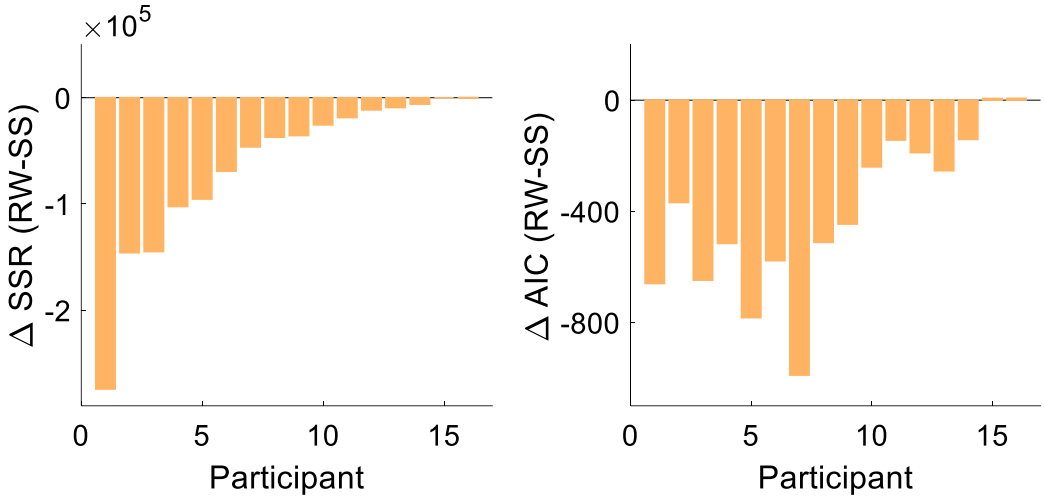

Figure S2. Model comparison. The sum of squares residuals (SSR) and Akaike Information Criterion (AIC) difference between Rescorla-Wagner (RW) and the state-space (SS) models for each participant of Experiment 1.

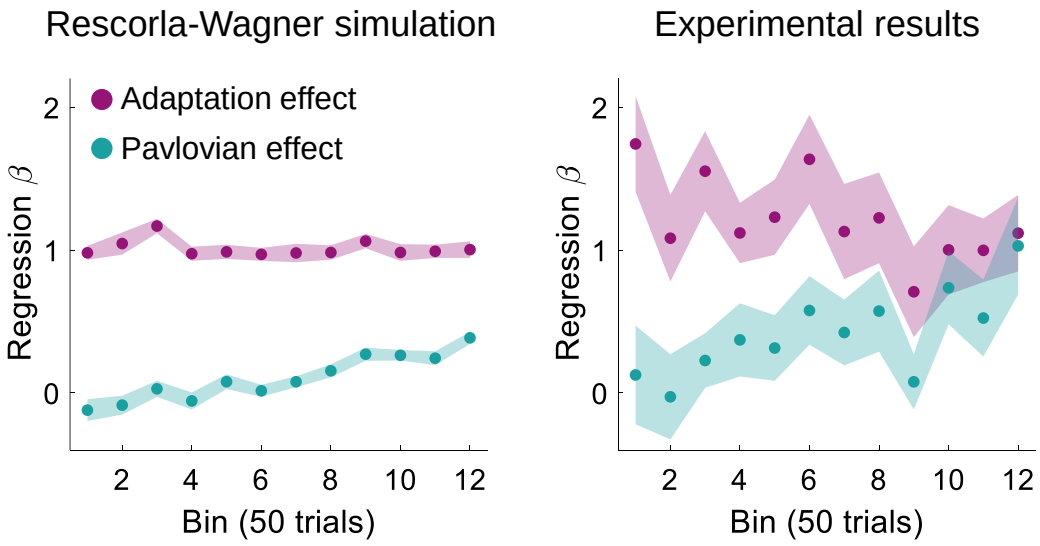

Figure S3. Dynamics of adaptation and Pavlovian effects. Time courses of the mean weights (regression *β*) of the adaptation (trial *n-1*, purple) and Pavlovian (trial *n*, cyan) effects in Experiment 1 as predicted by the Rescorla-Wagner model (left), and the actual experimental results (right). Shaded regions represent SEM.

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FIGURE CAPTIONS

Figure 1. Reaching Task. (A) Clamped-feedback induces implicit adaptation. (B) Adaptation described as a conditioning process. (C) Participants reach to a single target (blue dot), moving a cursor (white dot) from a start location (white circle). The target is displayed in a fixed location for the entire experiment (location varied across participants), and the direction of the cursor trajectory is fixed ("clamped") on all trials. After a random delay, a tone and/or a light (white frame) is presented, serving as the movement imperative. This cue persists for the duration of the movement.

Figure 2. Experiment 1: Differential Conditioning. (A) Trial types. A 15° clamp (CW/CCW, counterbalanced across participants) was associated with CS+ and a 0° clamp with CS- (counterbalancing the associations with the tone and light across participants). (B) Experimental protocol. CS+ (e.g., tone) and CS- (e.g. light) trials were randomly interleaved. Clamped feedback (±15°/0°) was presented during the acquisition phase (white background), and no feedback was provided during the probe phase (gray). (C) Mean hand angle time course (N=16). (D) Simulation results for trial-by-trial change (Δ) in hand angle during acquisition. While the state-space model predicts only an adaptation effect (main effect of trial *n-1*, dark vs light blue), the Rescorla-Wagner model also predicts a Pavlovian effect (main effect of the presented CS on the current trial *n*, filled vs empty bars). (E) Experimental results for trial-by-trial Δ hand angle during acquisition comport with the Rescorla-Wagner model simulations but not the state-space model simulations (left panel). The black outlined bar (right panel) presents the Pavlovian effect, i.e. the subtraction of hand angle changes between CS+ and CS- trials. (F, G) Similar to (D) and (E), respectively, but for the probe phase, showing a significant Pavlovian effect that is consistent with the Rescorla-Wagner model. Shaded regions and error bars represent SEM. Dots represent individual participants.

Figure 3. Experiment 2: Compound Conditioning. (A, B) During acquisition, a 15° clamp was associated with a compound CS: Tone and light were presented simultaneously as movement imperatives. During the probe phase, no feedback was provided, and the CSs were presented either together (Compound CS) or alone (Single CS; tone or light). (C) Mean hand angle time course (N=22). (D) Simulation results for trial-by-trial Δ hand angle during the probe phase for the compound CS (filled bar) and each of its elements (empty bars). Unlike the state-space model, the Rescorla-Wagner model predicts a positive relative change for the compound CS on the current trial *n* and a negative relative change for each element. (E) Experimental results for the Δ hand angle during the probe are in line with the Rescorla-Wagner model. (F) Scatter plot showing the relationship between individuals' responses to the elemental CSs (the dotted black line represents the unity line). Shaded regions and error bars represent SEM. Dots represent individual participants.

Figure S1. Simulations of Pavlovian effects in differential conditioning. Simulations of current trial CS effect, i.e. the difference between the change in hand angle on CS+ and CS- trials, for the acquisition (top panel) and probe (bottom panel) phases of Experiment 1, as predicted by the state-space (left) and Rescorla-Wagner (right) models. Contours represent mean±SEM of the Pavlovian effect from Experiment 1.

Figure S2. Model comparison. The sum of squares residuals (SSR) and Akaike Information Criterion (AIC) difference between Rescorla-Wagner (RW) and the state-space (SS) models for each participant of Experiment 1.

Figure S3. Dynamics of adaptation and Pavlovian effects. Time courses of the mean weights (regression β) of the adaptation (trial n-1, purple) and Pavlovian (trial n, cyan) effects in Experiment 1 as predicted by the Rescorla-Wagner model (left), and the actual experimental results (right). Shaded regions represent SEM.

Figure 1

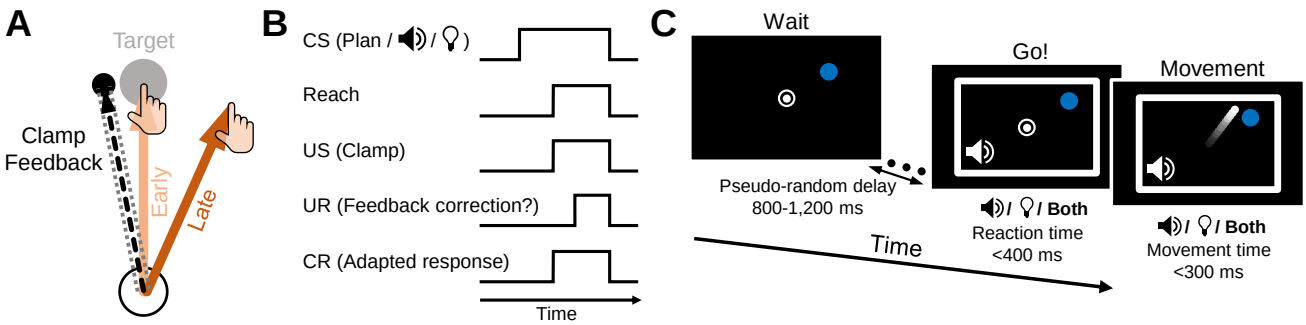

A
Target
Clamp
Feedback
Early
Late
B
CS (Plan / /)
Reach
US (Clamp)
UR (Feedback correction?)
CR (Adapted response)
Time
C
Wait
Pseudo-random delay
800-1,200 ms
Go!
/ / Both
Reaction time
<400 ms
Movement
/ / Both
Movement time
<300 ms
Time

Figure 2

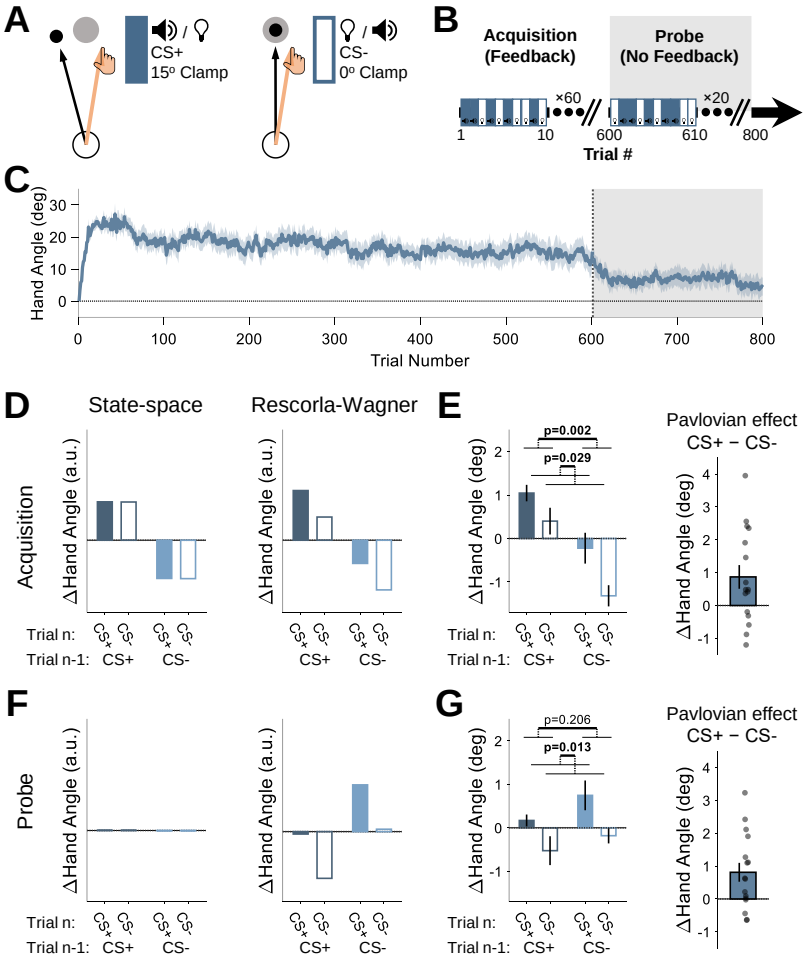
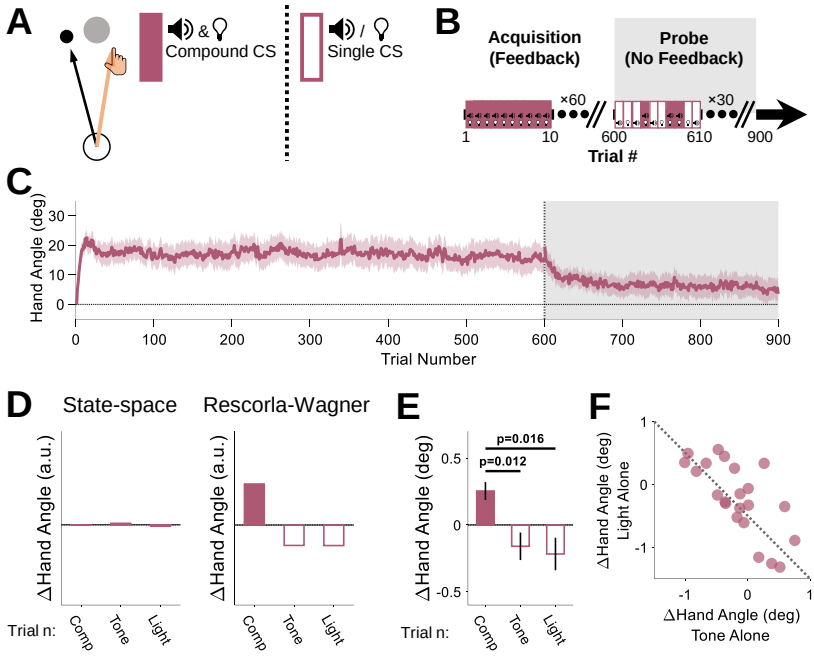

A
CS+
15º Clamp
CS-
0º Clamp
B
Acquisition
(Feedback)
Probe
(No Feedback)
×60
×20
1
10
600
610
800
Trial #
C
Hand Angle (deg)
Trial Number
D
State-space
Rescorla-Wagner
Acquisition
ΔHand Angle (a.u.)
Trial n:
Trial n-1:
CS+
CS-
E
p=0.002
p=0.029
ΔHand Angle (deg)
Pavlovian effect
CS+ − CS-
F
Probe
G
p=0.206
p=0.013

Figure 3


A
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Single CS
B
Acquisition
(Feedback)
Probe
(No Feedback)
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610
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Trial #
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Hand Angle (deg)
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20
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100
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Trial Number
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State-space
Rescorla-Wagner
ΔHand Angle (a.u.)
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Tone
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p=0.016
p=0.012
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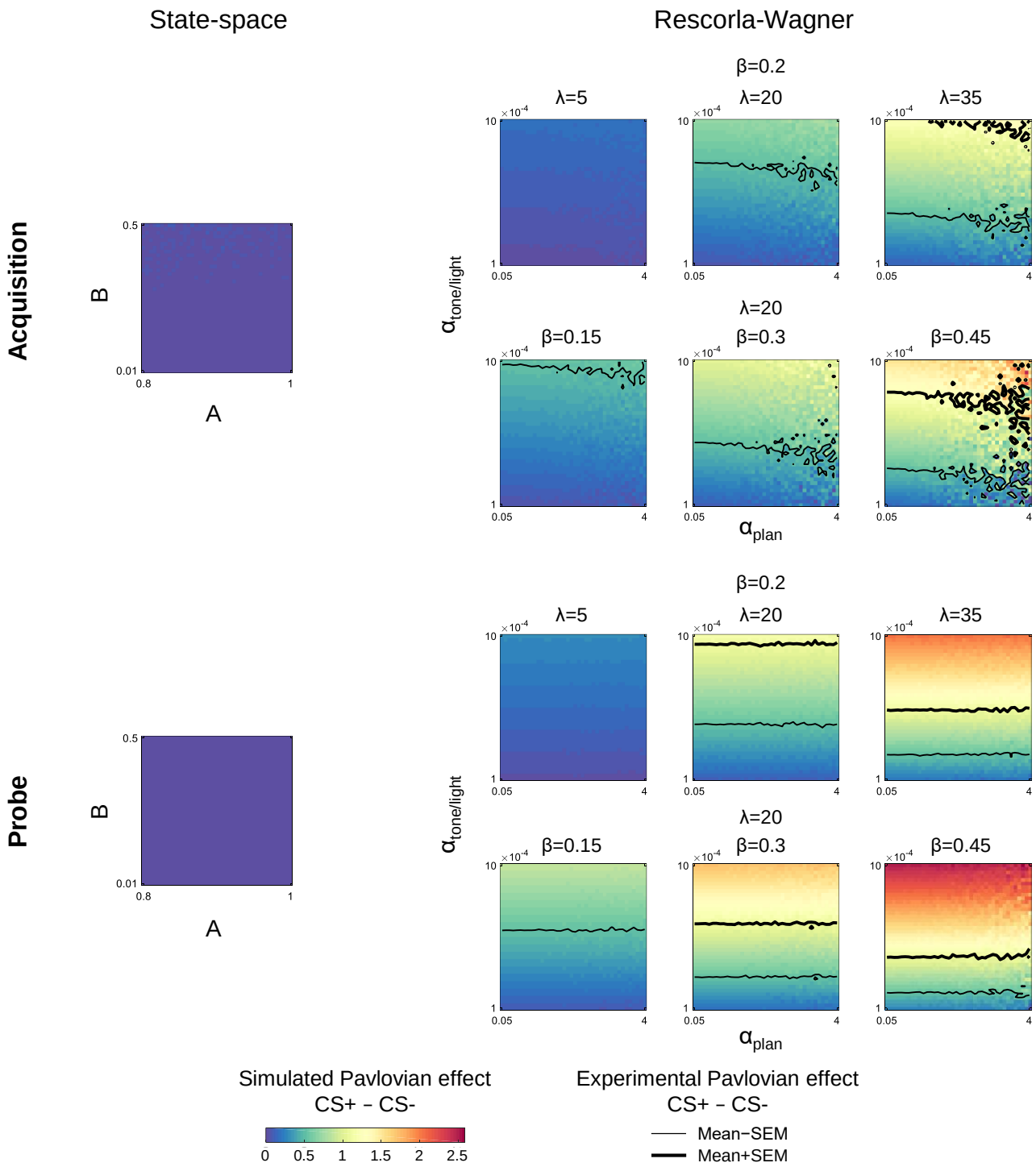
Figure S1


State-space
Rescorla-Wagner
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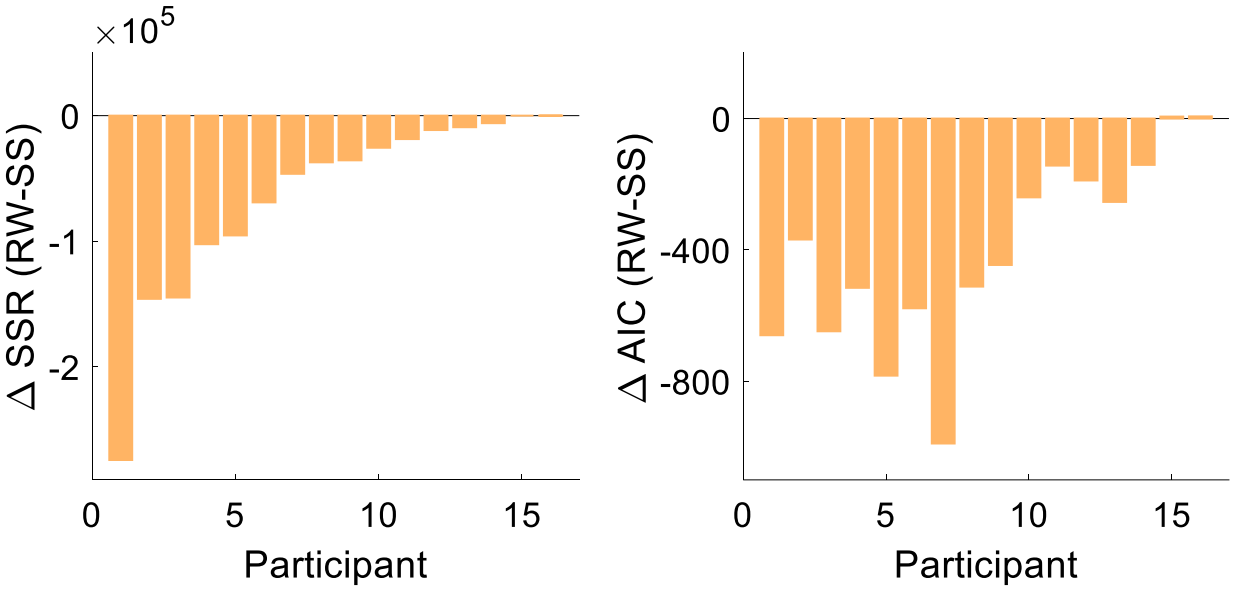
λ=35
λ=20
β=0.15
β=0.3
β=0.45
$\alpha_{tone/light}$
α_{plan}
$\times 10^{-4}$
10
1
0.05
4
Simulated Pavlovian effect
CS+ – CS-
0
0.5
1
1.5
2
2.5
Experimental Pavlovian effect
CS+ – CS-
Mean−SEM
Mean+SEM

Figure S2


×10^5
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Δ SSR (RW-SS)
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Participant
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Δ AIC (RW-SS)
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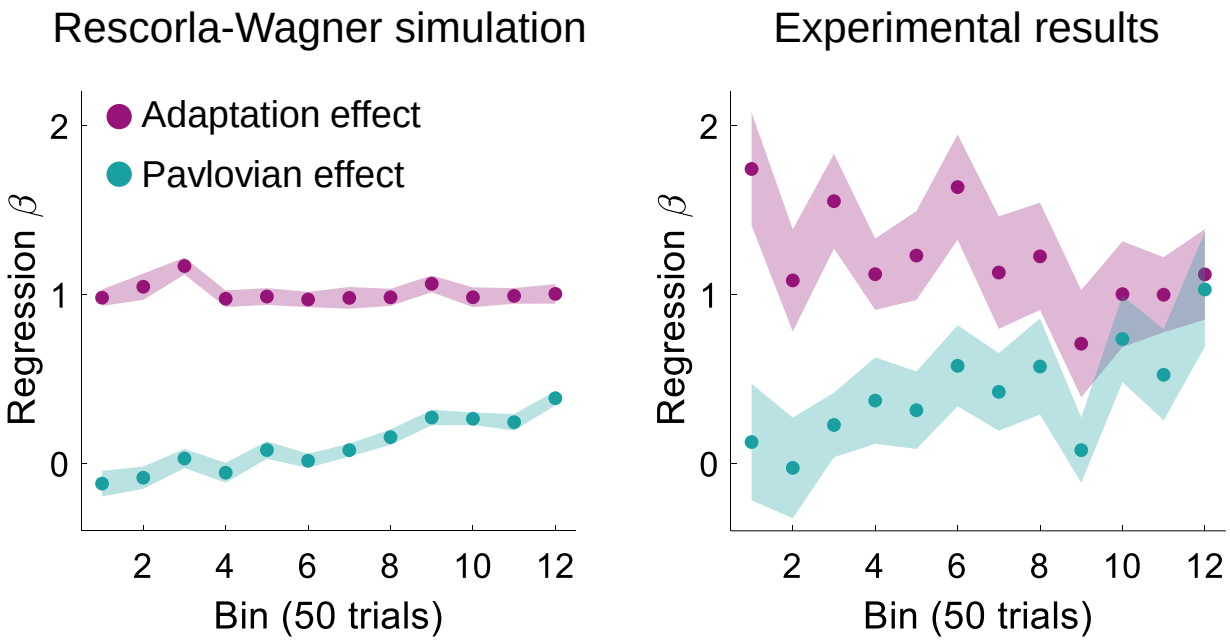
10
15
Participant

Figure S3


Rescorla-Wagner simulation
Experimental results
Adaptation effect
Pavlovian effect
Regression β
Bin (50 trials)
2
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