Contextual effects in motor adaptation adhere to associative learning rules

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ABSTRACT

Two influential paradigms, eyeblink conditioning and motor adaptation, have deepened our understanding of the theoretical and neural foundations of sensorimotor learning. Although both forms of error-based learning are dependent on the cerebellum, the two literatures typically operate within distinct theoretical frameworks. For eyeblink conditioning, the focus is on the formation of associations between an error signal and arbitrary stimuli. For adaptation, the error signal is used to modulate an internal model of a sensorimotor map for motor planning. Here we take a step towards an integrative account of these two forms of learning, examining the relevance of core concepts from associative learning for motor adaptation. Using a task that drives implicit adaptation of reaching movements, we paired movement-related feedback with neutral auditory or visual cues that served as conditioning stimuli (CSs). Trial-by trial changes in feedforward movement kinematics exhibited two key signatures of associative learning: Differential conditioning and compound conditioning. Moreover, after compound conditioning, a robust negative correlation was observed between responses to the two elemental CSs of the compound (i.e., overshadowing), consistent with the additivity principle posited by models of associative learning. Computational modeling demonstrated that these results could not be captured by conventional, context-insensitive algorithms used to describe motor adaptation. Associative learning effects in motor adaptation provide a proof-of-concept for linking cerebellar-dependent learning paradigms within a common theoretical framework.

SIGNIFICANCE STATEMENT

Motor adaptation is a cerebellar-dependent process, describing how the motor system remains calibrated in response to environmental and bodily changes. Another cerebellar-dependent learning phenomenon, eyeblink conditioning, is viewed as an associative learning process. Here we sought to bringing together these two approaches for studying sensorimotor learning. We

demonstrate that core associative learning phenomena are manifest during motor adaptation, pointing to a common framework for these distinct cerebellar-dependent motor learning processes.

INTRODUCTION

A hallmark of many motor learning tasks is the use of error information to improve performance. Sensorimotor errors not only signal that an action has not been properly executed but can provide information on how the output of the system should be changed to increase the likelihood of future success in a similar context. Two paradigmatic tasks for studying error-based learning are sensorimotor adaptation and eyeblink conditioning. Sensorimotor adaptation refers to the gradual adjustment of movements in response to changes in the environment or body. The key principle in this process is that on each trial, sensorimotor prediction errors are used to update an internal model of a sensorimotor mapping to help keep the sensorimotor system precisely calibrated (Shadmehr and Krakauer, 2008; Wolpert et al., 1995; Wolpert and Ghahramani, 2000). In eyeblink conditioning, a form of classical conditioning (Pavlov, 1927), learning centers on the formation of associations between an aversive stimulus (i.e., an error signal) and arbitrary cues. In a standard variant of this task, an aversive air puff to the cornea (unconditioned stimulus, or US) 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). The CR is adaptative, mitigating the anticipated aversive sensory consequences of the US.

In addition to serving as paradigmatic examples of implicit, error-based motor learning (Clark et al., 2002; Clark and Squire, 1998; Mazzoni and Krakauer, 2006; Morehead et al., 2017), sensorimotor adaptation and eyeblink conditioning share core properties. First, although one task

involves active planning (motor adaptation) and the other passive conditioning of a reflex (eyeblink conditioning), both involve a learning signal based on a sensorimotor error that must occur close in time to an initial prediction to drive learning (Brudner et al., 2016; Kitazawa et al., 1995; Rasmussen et al., 2008; Schneiderman and Gormezano, 1964; Schween and Hegele, 2017; Shadmehr et al., 2010). Second, both are strongly associated with the cerebellum (Donchin et al., 2011; Garcia et al., 1999; Gerwig et al., 2007; Izawa et al., 2012; Kim and Thompson, 1997; Popa et al., 2016; Schlerf et al., 2012).

While these parallels suggest a link between sensorimotor adaptation and eyeblink conditioning, it is surprising that the two literatures have generally operated within distinct theoretical frameworks. For adaptation, the focus has been on how an error signal is used to directly update a motor command and the anticipated sensory consequences of that command. For eyeblink conditioning, the focus has been on how an error signal is used to build an association between an arbitrary stimulus (the CS) and an aversive event (the US) to produce a predictive, adaptive response (the CR). This last point highlights one aspect of apparent divergence between adaptation and conditioning: A prominent feature of sensorimotor adaptation has been the finding that, at least when putatively restricted to implicit learning, arbitrary cues are not effective for this form of learning. For example, people do not differentially adapt their reaching movements to two opposing perturbations when the perturbation is signaled by a distinct color cue in the environment (Howard et al., 2012, 2013; Gandolfo et al., 1996).

Subsequent work has shown that contextual cues can be highly effective when the cue is directly relevant to the movement. For example, people can simultaneously adapt to opposing perturbations if the context is established by movements prior to, or following, the perturbed segment of a reach (Howard et al., 2015, 2012; Sheahan et al., 2016). In these situations, the contextual cues are thought to affect learning because the cues are incorporated into the motor plan itself (Howard et al., 2013, 2012). This notion contrasts with classical conditioning, where

predictive, arbitrary sensory cues need not have a direct relationship to the events they predict, accruing associative value as long as they comply with strict timing requirements (Schneiderman and Gormezano, 1964; Smith et al., 1969).

Here we take a first step toward bridging these two worlds by applying some key theoretical concepts and design features of classical conditioning studies to a visuomotor rotation task. First, we test the idea that arbitrary sensory cues can indeed shape motor adaptation, even though they have no direct link to motor commands. Second, we test the hypothesis that the effect of these cues on adaptation will adhere to established principles of associative learning. By demonstrating these parallels between conditioning and motor adaptation, we offer a more parsimonious framework for understanding these disparate cerebellar-dependent learning processes.

RESULTS

We modified a visuomotor rotation task to ask if implicit motor adaptation exhibits associative behavior when a perturbation is paired with an arbitrary sensory cue. Participants were asked to reach from a start location to a target with movement feedback provided by a cursor (Fig. 1A). Drawing on classic work in animal learning (Pavlov, 1927; Rescorla and Wagner, 1972), we presented sensory events (a tone or light stimulus) as imperative cues for movement initiation. The use of a neutral stimulus to cue movement initiation provides a means to establish a tight temporal link between these arbitrary cues – the CSs in the task – and sensorimotor feedback, the US. This temporal linkage of the CS and US, where the CS onset precedes the US and the two events occur close in time, are prerequisites for cerebellar-dependent delay conditioning (Schneiderman and Gormezano, 1964). To promote this timing constraint, a warning was given if the participant did not move within 400 ms of the imperative, reminding them to initiate the

movement faster. Participants complies with this requirement, exhibiting rapid reaction times (Mean ± STD: 287±45.2 ms).

Rather than impose a typical visuomotor perturbation on the feedback (e.g., rotate the cursor relative to the true hand position), we opted to use “clamped” feedback. In this technique, which is designed to isolate implicit motor adaptation, the cursor path is not tied to the direction of the reach but rather follows an invariant (“clamped”) path, with the radial position of the cursor corresponding to the radial position of the hand (Morehead et al., 2017; Shmuelof et al., 2012). As in past studies with clamped feedback, the participant was fully informed of the clamp manipulation and instructed to ignore the task-irrelevant cursor and reach straight to the target on all trials. As such, this method eliminates the potentially confounding effects of strategic processes (McDougle et al., 2016; Kim et al., 2020). Nonetheless, participants’ reach angles gradually shift in the direction opposite to the clamp and shows the cardinal signatures of implicit motor adaptation without awareness (Morehead et al., 2017; Kim et al., 2018, 2019; Parvin et al., 2018; Tsay et al., 2020a, 2020b, 2021a, 2021b; Avraham et al., 2021; Poh et al., 2021; Vandevoorde and Orban de Xivry, 2019; Yin and Wei, 2020).

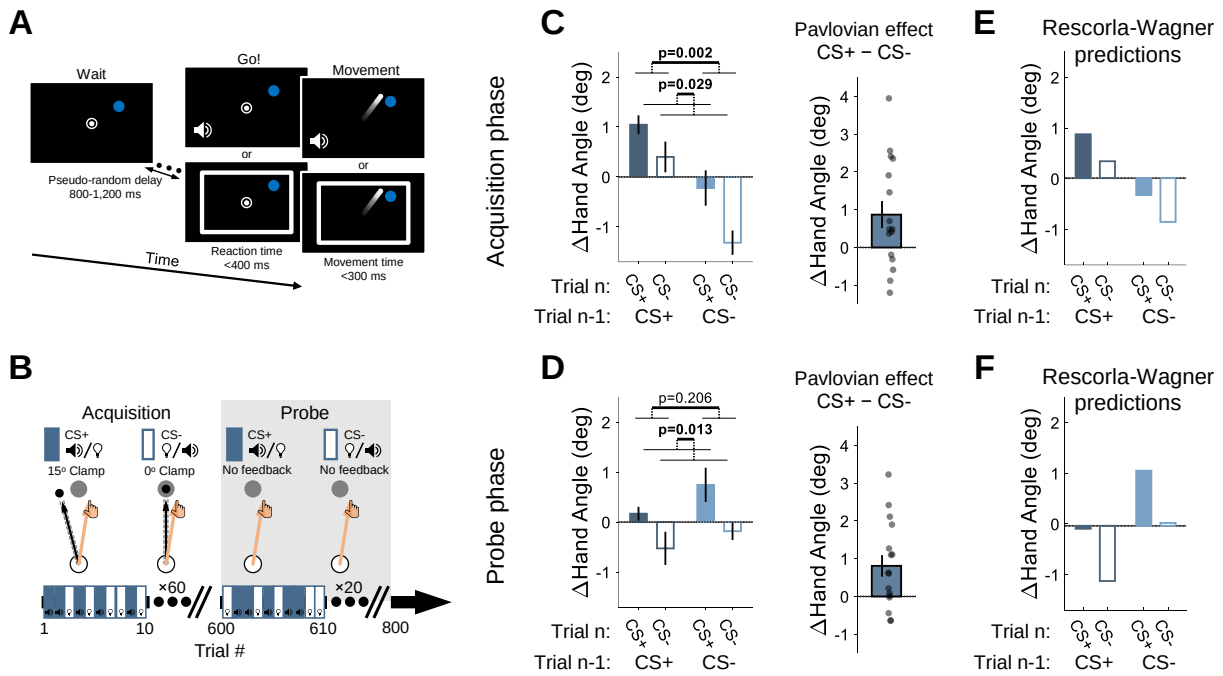

Figure 1. Experiment 1: Differential Conditioning.

(A) Reaching task. Participants reach from a start location (white circle) to a target (blue dot). Online feedback is provided by a cursor (white dot). 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 or a light (white frame) is presented, serving as the movement imperative. The cue persists for the duration of the movement. (B) Experimental protocol. During acquisition (white background), a 15° clamp (CW/CCW, counterbalanced across participants) was associated with CS+ (e.g., a tone) and a 0° clamp with CS- (e.g., a light; counterbalancing the associations with the tone and light across participants). During the probe phase (gray background), CS+ and CS- were presented with no feedback. Throughout the entire experiment, CS+ and CS- trials were randomly interleaved. (C, D) Experimental results (N=16) for trial-by-trial change (Δ) in hand angle during the acquisition (*C*) and probe (*D*) phases. Left panels present analysis results for an adaptation effect (main effect of trial *n-1*, dark vs light blue) and a Pavlovian effect (main effect of the presented CS on the current trial *n*, filled vs empty bars). The black outlined bar (right panel) presents the Pavlovian effect, i.e., the subtraction of hand angle changes between CS+ and CS- trials. (E, F) Rescorla-Wagner model simulation results during the acquisition (*E*) and probe (*F*) phases are consistent with the experimental results. Error bars represent SEM. Dots represent individual participants.

Motor adaptation is modulated by arbitrary sensory cues

In differential conditioning, one CS is paired with the US (CS+) and another CS is presented without the US (CS-). Thus, only the CS+ should become associated with the US and result in a CR. To implement this in Experiment 1, we used two arbitrary cues for the CS's – a tone or a light cue – and clamped cursor feedback for the US's (Morehead et al., 2017). Rather than vary the presence or absence of feedback, we manipulated the trajectory of the cursor feedback to signal the presence or absence of an error: For the CS+ condition, the feedback cursor followed a clamped path that was rotated from the target by 15° (i.e., error/US present); for the CS- condition, the feedback cursor always moved directly to the target (i.e., error/US absent). The CR in this scenario is the angular deviation of the movement in the opposite direction of the 15° clamp.

During a 600-trial acquisition phase, CS+ and CS- trials were randomly interleaved. Participants exhibited a marked change in movement direction during this phase, reaching an asymptote of ~15° (Fig. S1A). This rapid adaptation is consistent with previous adaptation studies, particularly those in which the target appears at a fixed location (Bond and Taylor, 2015; Day et al., 2016; McDougle et al., 2015, 2017; Poh et al., 2021).

The main analysis centered on trial-by-trial changes in hand angle. The change in hand angle from trial *n-1* to trial *n* is normally dictated by the feedback experienced in trial *n-1*. Thus, following experience with an error on CS+ trials, participants should show increased adaptation (a positive change in hand angle), and following no error on CS- trials, decreased adaptation. We refer to these trial-by-trial changes as the "adaptation effect", the standard measure of learning in sensorimotor adaptation studies. However, the conditioning framework makes a critical additional prediction: The CS+ and CS- should differentially modulate the hand angle on trial *n* itself. That is, the presentation of the light or tone should produce a CR associated with that cue, leading to a difference in hand angle between the two cues that is independent of the feedback during the

previous trial. We refer to this as the “Pavlovian effect.” Importantly, if implicit adaptation is not sensitive to arbitrary contextual cues, we expect to only observe an adaptation effect.

A robust adaptation effect was observed (Fig. 1C, left panel): Trial-by-trial changes in reaching direction (Δ hand angle) were significantly affected by the CS presented on the previous trial [$F(1,15)=13.3$, $p=0.002$, $\eta_p^2=0.47$] 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). This is the canonical signature of incremental motor adaptation.

The critical test of our hypothesis centers on the Pavlovian effect. As shown in Figure 1C (both panels), the results revealed clear Pavlovian effects: 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 [$F(1,15)=5.83$, $p=0.029$, $\eta_p^2=0.28$]. This effect provides a novel demonstration that arbitrary sensory cues can lawfully influence implicit motor adaptation.

We also observed an interaction between CS identity on trials *n-1* and *n* [$F(1,15)=7.11$, $p=0.018$, $\eta_p^2=0.32$]. 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 likely reflects an asymmetry between the rate of the acquisition and extinction processes once CS-US associations are established. That is, the state 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.

We note that the visual 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 online feedback responses. This explanation is unlikely given that the movements were quite rapid ([Mean±STD], 103±31.2 ms). To directly assess the online correction hypothesis, we calculated the difference in hand angle 50 ms after movement initiation and at the radial distance of the target. There was no overall change in hand angle between the time points (-0.32°±2.92°), and no significant difference between CS+ and CS- trials on this metric [t(15)=-0.47, p=0.640, *d*=-0.12]. Thus, our results appear to pertain exclusively to feedforward learning.

Following the acquisition phase, participants completed a probe phase in which CS+ and CS- trials were randomly presented in the absence of any visual feedback (no US). This phase provides a "clean" test for associative learning effects since it removes trial-by-trial effects that arise from the differential feedback given during CS+ and CS- acquisition trials. Here too we observed a significant Pavlovian effect: Although there was an overall decrease in hand angle across the probe phase (i.e., a partial washout of adaptation, Fig. S1A), there was a significant main effect of the CS presented on trial *n* [F(1,15)=7.98, p=0.013, η_p^2=0.35] (Fig. 1D), with a relative increase in hand angle on CS+ trials and a decrease on CS- trials. Moreover, there was neither an effect of the trial *n-1* CS [F(1,15)=1.74, p=0.206, η_p^2=0.10] nor a trial *n-1* x *n* interaction [F(1,15)=0.25, p=0.621, η_p^2=0.02], consistent with trial-by-trial adaptation being dependent on error feedback.

Importantly, the Pavlovian effect did not appear to be driven by explicit awareness of the CS-US contingency. A post-experiment survey was used to classify participants as either aware or unaware of the CS-US associations (see *Methods*). Participants who reported being aware of the contingencies (N=7) did not show a different Pavlovian effect compared to those who reported being unaware (N=9) in either the acquisition (t(14)=-0.333, p=0.744, BF_{10}=0.446, *d*=-0.17) or probe (t(14)=-0.081, p=0.937, BF_{10}=0.431, *d*=-0.04) phases. A similar null effect of awareness on the strength of Pavlovian conditioning has also been reported in studies of human delay eyeblink conditioning (Clark and Squire, 1998).

In summary, the observed effects of context on implicit motor adaptation in both the acquisition and probe phases in Experiment 1 are consistent with differential conditioning effects observed in classical conditioning. Feedforward implicit motor adaptation – here operationalized as a type of CR – was differentially modulated by an arbitrary sensory CS+ versus CS-, with a greater response to the CS+, the cue that was paired with a visuomotor error.

The standard approach to describe motor adaptation is based on a "state-space" model in which the motor state is updated according to the error observed on the previous trial. The parameters of this model determine both the trial-by-trial retention of the previous state and the rate of learning from the error (see Eq. 3 in the *Methods*). By definition, a model of this form only predicts a behavioral change based on trial *n*-1 (i.e., an adaptation effect), where no change in hand angle is produced by the trial *n* CS; thus, this standard model cannot capture any context effects (e.g., our Pavlovian effect).

In contrast, the Rescorla-Wagner model, a classic model of associative learning, provides a straightforward account of context effects. It formalizes changes in conditioned responses via the modulation of (arbitrary) learned associations. Here, the associative strengths, *V*, of the conditioning stimuli are updated according to the learning rule (Eq. 1):

$$V^{[n]} = V^{[n-1]} + \alpha \cdot \beta \cdot SPE^{[n-1]}, \quad (1)$$

where *V* represents the associative strengths between the US and the CS. It is updated based on the sensory prediction error (*SPE*) presented on trial *n*-1. The *SPE* is defined as λ-$V^{[n-1]}$, where λ is the maximum conditioning (asymptotic) level of the US. β is the learning rate parameter of the US and α represents the salience of the CS. We note that the Rescorla-Wagner model does not provide a mechanistic account for error-correction itself (e.g., the fact that the motor system "knows" to update movements in the direction opposite of the error). For simplicity, we assume that the sign of the change in movement direction is determined by a specialized neural circuit

attempting to reduce directional motor errors (Hadjiosif et al., 2021; Herzfeld et al., 2018; Wolpert et al., 1998).

To illustrate that the Rescorla-Wagner model can capture differential conditioning behavior similar to the results observed in Experiment 1, we performed model simulations. The simulation results demonstrate both the adaptation effect and Pavlovian effect for the acquisition phase (Fig. 1E), as well as a clear Pavlovian effect for the Probe phase (Fig. 1F). Importantly, the behavioral signature of differential conditioning, the larger changes in hand angle on CS+ trials compared to CS- trials, holds for essentially all combinations of parameters in the Rescorla-Wagner model (Fig. S2, left side). In contrast, there are no parameter combinations for the state-space model that can produce this behavior (Fig. S2, right side). As noted above, the failure of the state-space model should be expected given that it has no mechanism for handling contextual effects (we return to this point in the *Discussion*).

To formally compare the Rescorla-Wagner and state-space models in terms of the observed results, we conducted a model comparison by fitting each participant's data with the two models. The Rescorla-Wagner model provided a better fit to the data than a standard state-space model (Fig. S3; *t*-test comparing sum of squared residuals, $t(15)=-3.62$, $p=0.003$, $d=-0.90$; *t*-test comparing Akaike Information Criterion (AIC) values, $t(15)=-6.44$, $p<0.001$, $d=-1.61$).

An additional analysis provided further support for an associative learning account of the results of Experiment 1. The Rescorla-Wagner model not only provides a framework for understanding how associations can be formed with arbitrary stimuli, but can also capture how the strength of these associations is constrained by the relevance of the cues; for instance, gustatory cues are much more likely to be associated with an internal state (e.g., nausea) than a visual cue (Garcia and Koelling, 1966). In the current study, the clamped feedback (the US) is a highly relevant stimulus for reaching; as such, we should expect it to have an immediate strong influence on motor behavior. In contrast, the imperative cues, the tone and light (the CSs) have

no natural relevance for reaching; as such, their contribution to the CR should initially be quite modest, gradually increasing over time (Fig. 2A). To test this prediction, we examined the time-course of the adaptation and Pavlovian effects during acquisition using a linear mixed model analysis. As expected, at early stages, the adaptation effect emerged quickly whereas the contribution of the Pavlovian effect was small. Over experience, the relative contribution of the two effects reversed (Type and Bin interaction effect: $F(1,365)=16.7$, $p<0.001$): The Pavlovian effect gradually grew (mean slope, [95% CI]; 0.14, [0.04 0.24]) at the expense of the adaptation effect, which eventually exhibited a reduced contribution (-0.15, [-0.25 -0.05]) (Fig. 2B). We note that both the decrease in the adaptation effect and the increase in the Pavlovian effect are not captured by a typical state-space model (Fig. S4).

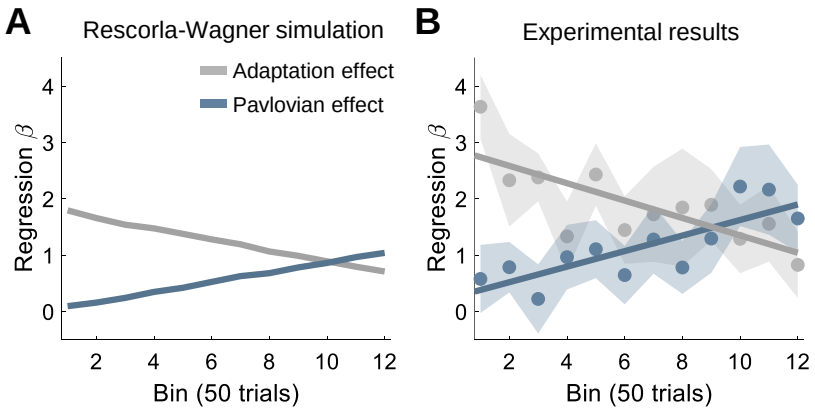

Figure 2. Dynamics of adaptation and Pavlovian effects.

Time course of the mean weights (regression *β*) of the adaptation (trial *n-1*, grey) and Pavlovian (trial *n*, blue) effects in Experiment 1 as predicted by the Rescorla-Wagner model (A) and derived from fits of the experimental results (B). Solid lines in *B* represent least squares regression lines. Shaded region represent SEM.

Additivity principle in response to compound stimuli is observed in motor adaptation

The differential conditioning results of Experiment 1 show that implicit motor adaptation manifests a prominent feature of classical conditioning, the gradual associability of an error signal with arbitrary sensory cues. In Experiment 2, we tested a second core phenomenon of associative learning, the principle of additivity (Mackintosh, 1976; Pavlov, 1927; Rescorla and Wagner, 1972). This principle is based on the idea that there is an associative capacity for a given US – the *V* term in the Rescorla-Wagner equation. Multiple CSs can become associated with a given US, but the combined associative strength is bounded by *V*. As a result of this capacity constraint, CSs effectively compete with one another, with the associative strength split among multiple cues.

The classic method to test for additivity is compound conditioning, where two or more stimuli are presented simultaneously to form a "compound" CS (Eq. 2). When paired with a US, this compound CS will come to elicit CRs. Importantly, the associative strength of the Compound CS (V_{comp}) is the sum of the associative strengths of the elemental CSs (V_i), where *nS* in Eq. 2 represents the number of elements forming the Compound CS. Consequently, 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.

$$(2)\ V_i^{[n]} = V_i^{[n-1]} + \alpha_i \cdot \beta \cdot (\lambda - V_{comp}^{[n-1]});\ V_{comp}^{[n-1]} = \sum_{i=1}^{nS} V_i^{[n-1]}$$

The additivity principle has received ample support in behavioral and neural studies of associative learning (Giurfa, 2007; Kehoe et al., 1994; Kehoe and Schreurs, 1986; Rescorla and Wagner, 1972; Weiss, 1972), but has not, to our knowledge, been tested in motor adaptation. In Experiment 2 we used a compound conditioning design pairing a 15° error clamp stimulus with a compound CS (simultaneous presentation of the tone and light; Fig. 3A) on all trials during the acquisition phase. As in Experiment 1, we again observed robust adaptation in the acquisition phase, manifest as a change in hand angle in the direction opposite to the clamp (Fig. S1).

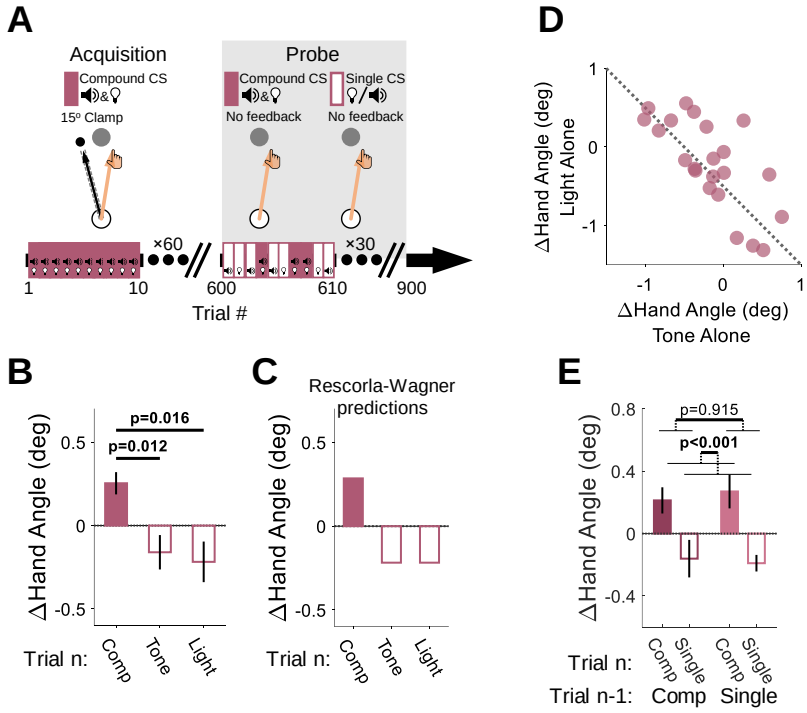

Figure 3. Experiment 2: Compound Conditioning.

(A) During acquisition, a tone and light were presented simultaneously (Compound CS), serving as the imperative signal for the reaching movement. They were paired on all trials with a 15° clamp. During the probe phase, no feedback was provided, and the CSs were presented either together (Compound CS) or alone (Single CS; tone or light). (B) Experimental results (N=22) for the Δ hand angle during the probe phase, showing a positive relative change for the compound CS on the current trial *n* (filled bar) and a negative relative change for each of its elements (empty bars). (C) Predictions from the Rescorla-Wagner model for trial-by-trial Δ hand angle during the probe phase. Note that the two elements were assumed to have equal weight in the simulation. (D) Scatter plot showing the between-participant trade-off in terms of the associative strength of the two CSs (the dotted black line represents the unity line). (E) The Δ hand angle after pooling the two single-CS conditions to measure the effects of the previous CS type (compound versus singleton, dark and light pink, respectively) and current CS (filled and empty bars). Error bars represent SEM.

The critical test in this experiment comes from the probe phase. Here, the clamped feedback was eliminated, and the imperative was either the original compound CS, or just the

tone or light alone. We observed a significant Pavlovian effect of CS type on these no-feedback trials [$F(2,42)=4.78$, $p=0.014$, $\eta_p^2=0.19$], with larger hand angles observed on compound CS trials relative to the tone-alone or light-alone trials, conforming to the first prediction of the additivity principle (Fig. 3B, 3C). Crucially, the additivity principle posits 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) given that there is a capacity limit of associability (*V*). This prediction was strikingly confirmed in an analysis of the hand angle changes on tone-alone and light-alone trials: Participants who were more sensitive to the tone stimulus were less sensitive to the light stimulus, and *vice versa* (Fig. 3D, Pearson correlation: $r=-0.72$, $p<0.001$).

As in Experiment 1, since the probe phase of Experiment 2 consisted of different types of CSs presented randomly across trials, the behavior for a given trial should reflect not only the CS on trial *n* but also the motor state on trial *n-1* (which is also influenced by the CS on that trial). As a further test of compound conditioning, we pooled the two single-CS conditions to measure the effects of the previous and current CS type (singleton versus compound) on the observed changes in hand angle. We again observed the Pavlovian effect [$F(1,21)=21.2$, $p<0.001$, $\eta_p^2=0.50$]: There was a relative increase in hand angle for the compound CS (Mean ± SE, 0.24°±0.06°) and a relative decrease for the single CSs (-0.18°±0.06°) (Fig. 3E). The main effect of the CS on trial *n-1* was not significant [$F(1,21)=0.012$, $p=0.915$, $\eta_p^2=0.00$] nor was the trial *n-1* × trial *n* interaction [$F(1,21)=0.276$, $p=0.605$, $\eta_p^2=0.01$], presumably due to the elimination of trial-by-trial adaptation given the absence of visual feedback in the probe phase.

DISCUSSION

Sensorimotor adaptation and eyeblink conditioning have provided foundational paradigms for the study of error-based sensorimotor learning. They have yielded a rich empirical foundation in the development of theoretical and neural models of learning and memory, particularly with respect to cerebellar function (Albus, 1971; Ito, 1984; Marr, 1969; Wolpert et al., 1998). Adaptation has typically been modeled from a control engineering perspective, centered on the idea that changes in behavior are driven by sensory prediction errors arising when the experienced feedback deviates from that predicted by a forward model operating on an efference copy of the motor command (Krakauer et al., 2019; Shadmehr and Krakauer, 2008; Wolpert and Flanagan, 2001). In contrast, eyeblink conditioning is treated as an associative learning process that can be driven by arbitrary sensory cues.

Our goal in the present study was to take a first step towards establishing explicit links between these two frameworks. To that end, we asked if core phenomena identified in the study of classical conditioning are operative in sensorimotor adaptation. We showed that visuomotor adaptation exhibited the hallmarks of both differential conditioning (Experiment 1) and compound conditioning (Experiment 2). These results provide the first evidence, to our knowledge, that pairing neutral stimuli (the tone and light) with distinct visuomotor outcomes can differentially influence implicit feedforward motor adaptation and do so in a manner consistent with the principles of associative learning rules.

The role of context in sensorimotor adaptation has been the subject of considerable debate. A number of labs have employed sensory cues, asking if these are sufficient to negate interference effects observed in response to interleaved opposing perturbations. The results from this work have generally shown that arbitrary visual cues such as differently colored cursors are ineffective, resulting in considerable interference between the perturbations (Gandolfo et al., 1996; Karniel and Mussa-Ivaldi, 2002; Howard et al., 2012, 2013; but see Krouchev and Kalaska,

2003; Osu et al., 2004; Addou et al., 2011). In contrast, postural and movement-related variables, such as different lead-in and follow-through movements, have been shown to act as reliable contextual cues for overcoming interference effects (Howard et al., 2012, 2013, 2015; Sheahan et al., 2016). One interpretation of these results has focused on the difference between static and dynamic cues, with the idea that the latter are incorporated into the motor state, allowing for the separation of distinct internal models (Howard et al., 2012, 2013).

In the current study, we found compelling contextual effects using static, arbitrary sensory cues. There are several key features of our design that differ from prior work with static cues. First, drawing on the eyeblink literature (Schneiderman and Gormezano, 1964; Smith et al., 1969), we imposed a strong temporal constraint on the interval between the CS (the contextual cue) and the US by having the cues serve as imperative signals and enforcing rapid response times. This strict temporal constraint was absent in prior studies; For example, in Howard et al. (Howard et al., 2013), the color cue was presented 1,000 ms before the imperative. Second, the salience of the arbitrary cues was arguably increased in the present study by having them serve as movement imperatives.

More broadly, we propose that an associative learning framework may provide a useful lens for understanding various aspects of sensorimotor adaptation. Consider a standard adaptation study in which there are no contextual cues: Adaptation is observed when feedback is perturbed while the participant reaches to a visual target. In such tasks, the target itself is not only a salient stimulus that defines the task goal and movement plan, but its onset usually serves as the imperative for movement initiation. Under these conditions, the target can be viewed as one (highly effective) CS. Given that RTs in these tasks are typically below 500 ms (Kim et al., 2019, 2018; Avraham et al., 2021), such designs might establish a tight temporal link between target appearance and movement, echoing (perhaps inadvertently) the CS-US temporal constraints essential for eyeblink conditioning (Schneiderman and Gormezano, 1964).

More precisely, we propose that it is the movement plan itself, rather than the target cue, that constitutes the primary CS in standard adaptation tasks. While the plan and target usually coincide, this is not always the case. For example, with a contingent visuomotor rotation, participants often deliberately aim away from the target, especially when the perturbation is large (Hegele and Heuer, 2010; Taylor et al., 2014). Recognizing this “re-aimed” plan as a CS provides a parsimonious account of a number of phenomena. First, generalization from adaptation is centered around the direction of the movement plan but not the target (Day et al., 2016; McDougle et al., 2017). This phenomenon echoes generalization effects seen in eyeblink conditioning, where variation of the CS (e.g., tone frequency) leads to parametric changes in CR probability (Siegel et al., 1968). Second, even in the absence of distinct contextual movements (e.g. follow-through), the activation of different motor plans can serve as efficient contextual cues, negating interference effects from opposing perturbations (Sheahan et al., 2016). Third, an emphasis on the plan is in accord with general models of cerebellar-dependent adaptation, where the prediction that constitutes the basis for sensory prediction error is computed using an efference copy of the motor intention (Blakemore et al., 2001; Gao et al., 2016; Kawato and Gomi, 1992; Wolpert et al., 1998).

To formally relate the eyeblink and adaptation worlds, we implemented the Rescorla-Wagner model, a classic associative learning model that has been widely employed in the classical and operant conditioning literature (Rescorla and Wagner, 1972). The success of this model to capture the general features of the current data sets should not be surprising since the model was developed to account for phenomena such as differential conditioning and compound conditioning. Thus, it was obvious to us that the Rescorla-Wagner model would provide better fits than the standard state-space model, given that the latter cannot capture contextual effects. In theory, the standard state-space model can be modified such that different sensory cues become associated with different states (Heald et al., 2018), allowing for context-dependent learning (e.g.,

differential conditioning). However, we emphasize that to account for compound conditioning, and in particular, the additivity principle, a state-space model would essentially have to become a variant of a Rescorla-Wagner model.

Although the Rescorla-Wagner model provides a ready account of how arbitrary sensory cues, visual targets, and even movement plans may provide a CS to drive adaptation, there are other phenomena in the sensorimotor adaptation literature that would not be accounted for by the model, at least in its simplest form. One such effect is spontaneous recovery, the re-manifestation of a previously adapted state in the absence of error feedback. A variant of the state-space model, one that allows for multiple states with different learning and forgetting rates, can capture spontaneous recovery (Smith et al., 2006). Second is the relationship between learning rate and environmental consistency; learning is faster in response to a consistent versus inconsistent perturbation (Albert et al., 2021; Avraham et al., 2020; Gonzalez Castro et al., 2014; Herzfeld et al., 2014; Hutter and Taylor, 2018). Here, the state-space model has been modified to allow the learning rate to vary with experience (Herzfeld et al., 2014). In its simplest form, the Rescorla-Wagner model cannot account for these effects. However, recent efforts to model associative learning have focused on how this framework may require more sophisticated, holistic computational approaches that complement simple associative mechanisms with inference processes (Collins and Frank, 2013; Gershman, 2015). A similar approach has been incorporated in a recent work looking at contextual effects in sensorimotor adaptation, and could successfully capture the aforementioned effects (Heald et al., 2020).

While our results highlight principles that address context-dependent motor adaptation, they do not speak to the error-correcting adaptation algorithm itself. Conventional models of this algorithm focus on the role of forward models in predicting future sensory states and updating motor commands to reduce sensory prediction errors, which are signed error signals (Wolpert and Ghahramani, 2000; but see Hadjiosif et al., 2021). Associative learning does not provide a

mechanism for the error correction process (e.g., a directional change in reaching movement given rotated feedback, or a well-timed eyeblink response to an airpuff); rather, it describes the association between a context and an error signal. Speculatively, motor adaptation perhaps operates as a lookup table of a multitude of context-error associations, built up from a lifetime of experience with subtle movement errors, with behavioral adjustments determined by a built-in, direction-sensitive error correcting mechanism (Herzfeld et al., 2018). A model of this form could bring sensorimotor adaptation closer to more classic models of cerebellar learning and plasticity (Albus, 1971; Ito, 1984; Marr, 1969). More generally, exploring the computational links between different sensorimotor learning tasks will be critical for understanding general principles of motor learning and their neural mechanisms.

METHODS

Participants

Thirty-eight healthy volunteers (aged 18-31 years; 31 females) participated in either Experiment 1 (N=16) or Experiment 2 (N=22). All participants were right-handed, as self-reported and 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.

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. 1A). 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), provided only 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 most studies of adaptation, the appearance of the target specifies both the movement goal (where to reach) and serves as the imperative (when to reach). From a classical conditioning perspective, the target should constitute a very salient CS given that its onset is temporally contingent 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, both of which 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 onset of the CS occurred following a pseudo-random and predetermined delay after the hand was positioned at the start location. This was done to mitigate predictions regarding the timing of the CS onset, and thus to enhance its salient role as an imperative. 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, slicing through the target. The CS was terminated when the hand reached 8 cm, the radial distance to the target (Fig. 1A). To minimize the delay between the onset of the CS and the US (the error clamp), the auditory message “start faster” was played whenever a 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. Given our objective to test the link between feedforward adaptation and classical conditioning, we sought to eliminate online feedback corrections. Participants were instructed to make rapid movements and the auditory message “move faster” was played whenever movement time exceeded 300 ms. The end of the movement was 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. 1B). 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.

The experimental software was custom written in Matlab (The MathWorks, Natick, MA), using the Psychtoolbox package (Brainard, 1997).

Experimental protocol

Both Experiments 1 and 2 included an acquisition phase and a probe phase. 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 baseline feedback and the target, movement plan, and any other contextual variables. A break of approximately 1-minute 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. 1B). 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 similar to that used in Experiment 1 with the following changes. First, the session consisted of 600 acquisition trials and 300 probe trials (Fig. 3A). Second, a compound CS, consisting of both the tone and light, served as the imperative throughout the acquisition phase, and was always paired with a 15° clamped feedback. Third, the probe phase (no visual feedback) consisted of 100 trials for each of the compound CS, tone alone CS, and light alone CS.

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 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 (Fig. S1), 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. 2B), we binned the hand angle data into epochs of 50 trials. Within each bin, we performed multiple regression analysis to test whether trial-to-trial change in hand angle can be predicted from the previous trial CS, the current trial CS and their interaction. Figure 2B presents the mean ± SEM regression β weights of all simulated time courses for the previous (adaptation effect) and current (Pavlovian effect) predictors. To evaluate statistically the changes in β weights for each type of effect across bins, we used a linear

mixed model (R statistical package: lmerTest), with Type (adaptation and Pavlovian) and Bin as fixed effects and participants as random effects.

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. We compared the Δ hand angle in response to the three CSs on trial *n* (compound CS, light alone, tone alone) 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 (Eq. 2). 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.

We report effect size using Cohen's *d* for all *t* tests and partial eta-squared (η_p^2) for the ANOVA. All of the measurements met the assumption of normality based on the Lilliefors test (Lilliefors, 1967).

Model simulations

Trial-by-trial reach angles were simulated using the Rescorla-Wagner model as a representative model for associative learning. In this model, the motor state is updated based on the associative strength (V) between the US (error signal) and all the CSs present on a given trial (Eqs. 1-2). The extent of learning is determined by the maximum conditioning level (λ), and the rate of behavioral change are determined by the learning rate of the US (β) and the salience of each presented CS (α). To illustrate the predictions of the model in Figures 1E, 1F and 3C, we chose parameters that result in qualitatively similar effects to the experimental results. For both Experiments 1 and 2, we set λ to 15, similar to the observed implicit adaptation asymptotes these experiments, as well as in other studies (Bond and Taylor, 2015; Morehead et al., 2017). The value of β was set to 0.12 (Exp. 1) or 0.02 (Exp. 2), the salience parameter (α) for the movement plan CS to 0.99, and both the tone CS and light CS to 0.002 (Exp. 1) or 0.1 (Exp. 2). These divergent salience values are consistent with the 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 of reaching to a target. The remainder of potential associative strength to the US is thus available for the tone and light CSs.

To demonstrate how the particular choice of parameters in the Rescorla-Wagner model influences the predicted Pavlovian 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_{goal}, α_{tone} and α_{light}. (For simplicity, we constrained α_{tone} and α_{light} to the same value.) Figure S2 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. In addition, we illustrated that a single-process state-space model, a standard model of motor adaptation, cannot capture these Pavlovian effects. In this model of motor adaptation, the motor state (x) is updated according to the following learning rule (Eq. 3):

$$x^{[n]} = A \cdot x^{[n-1]} + B \cdot SPE^{[n-1]} \quad (3)$$

where *SPE* is the sensory prediction error – the difference between the predicted and the actual sensory feedback – experienced on trial *n*-1, *A* is the retention factor, and *B* is the learning rate. For the simulation presented in Figure S2, the error was fixed to one of two values during the acquisition phase, either -15° on CS+ trials or 0° on CS- trials, and in the probe phase, it was set to 0° on all trials.

While the two models share similar features and parameters (e.g., learning rate of an error signal), 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, 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 simulate the dynamics of the adaptation and Pavlovian effects in differential conditioning (Fig. 2A, S4), and to compare it to the dynamics observed in the actual data, we simulated the trial-by-trial change in hand angle during acquisition (600 trials) according to the Rescorla-Wagner model (Eqs. 1 and 2) and the state-space model (Eq. 3), based on the schedules of CS+ and CS- trials that were presented to the participants (16 simulated time courses). For the Rescorla-Wagner model, we used the same parameters values that generated the simulation results presented in Figures 1E and 1F. For the state-space model, we set the *A* parameter to 0.9 and *B* to 0.12. We then did the same trial-by-trial regression analysis described above for the actual hand angle data (see *Data analysis*) with the exception that the dependent variable was now the simulated change in hand angle.

Model fitting and comparison

We conducted a *post-hoc* model comparison analysis (Fig. S2). In this analysis, we fit the Rescorla-Wagner model (Eqs. 1 and 2) and the standard state-space model (Eq. 3) to participants' hand angle time course data of 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 [-30, 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 goal, tone and light are unidentifiable, and both models make indistinguishable behavioral predictions during acquisition.

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FIGURE CAPTIONS

Figure 1. Experiment 1: Differential Conditioning.

(A) Reaching task. Participants reach from a start location (white circle) to a target (blue dot). Online feedback is provided by a cursor (white dot). 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 or a light (white frame) is presented, serving as the movement imperative. The cue persists for the duration of the movement. (B) Experimental protocol. During acquisition (white background), a 15° clamp (CW/CCW, counterbalanced across participants) was associated with CS+ (e.g., a tone) and a 0° clamp with CS- (e.g., a light; counterbalancing the associations with the tone and light across participants). During the probe phase (gray background), CS+ and CS- were presented with no feedback. Throughout the entire experiment, CS+ and CS- trials were randomly interleaved. (C, D) Experimental results (N=16) for trial-by-trial change (Δ) in hand angle during the acquisition (*C*) and probe (*D*) phases. Left panels present analysis results for an adaptation effect (main effect of trial *n-1*, dark vs light blue) and a Pavlovian effect (main effect of the presented CS on the current trial *n*, filled vs empty bars). The black outlined bar (right panel) presents the Pavlovian effect, i.e., the subtraction of hand angle changes between CS+ and CS- trials. (E, F) Rescorla-Wagner model simulation results during the acquisition (*E*) and probe (*F*) phases are consistent with the experimental results. Error bars represent SEM. Dots represent individual participants.

Figure 2. Dynamics of adaptation and Pavlovian effects.

Time course of the mean weights (regression *β*) of the adaptation (trial *n-1*, grey) and Pavlovian (trial *n*, blue) effects in Experiment 1 as predicted by the Rescorla-Wagner model (A) and derived

from fits of the experimental results (B). Solid lines in *B* represent least squares regression lines. Shaded region represent SEM.

Figure 3. Experiment 2: Compound Conditioning.

(A) During acquisition, a tone and light were presented simultaneously (Compound CS), serving as the imperative signal for the reaching movement. They were paired on all trials with a 15° clamp. During the probe phase, no feedback was provided, and the CSs were presented either together (Compound CS) or alone (Single CS; tone or light). (B) Experimental results (N=22) for the Δ hand angle during the probe phase, showing a positive relative change for the compound CS on the current trial *n* (filled bar) and a negative relative change for each of its elements (empty bars). (C) Predictions from the Rescorla-Wagner model for trial-by-trial Δ hand angle during the probe phase. Note that the two elements were assumed to have equal weight in the simulation. (D) Scatter plot showing the between-participant trade-off in terms of the associative strength of the two CSs (the dotted black line represents the unity line). (E) The Δ hand angle after pooling the two single-CS conditions to measure the effects of the previous CS type (compound versus singleton, dark and light pink, respectively) and current CS (filled and empty bars). Error bars represent SEM.

Figure 1

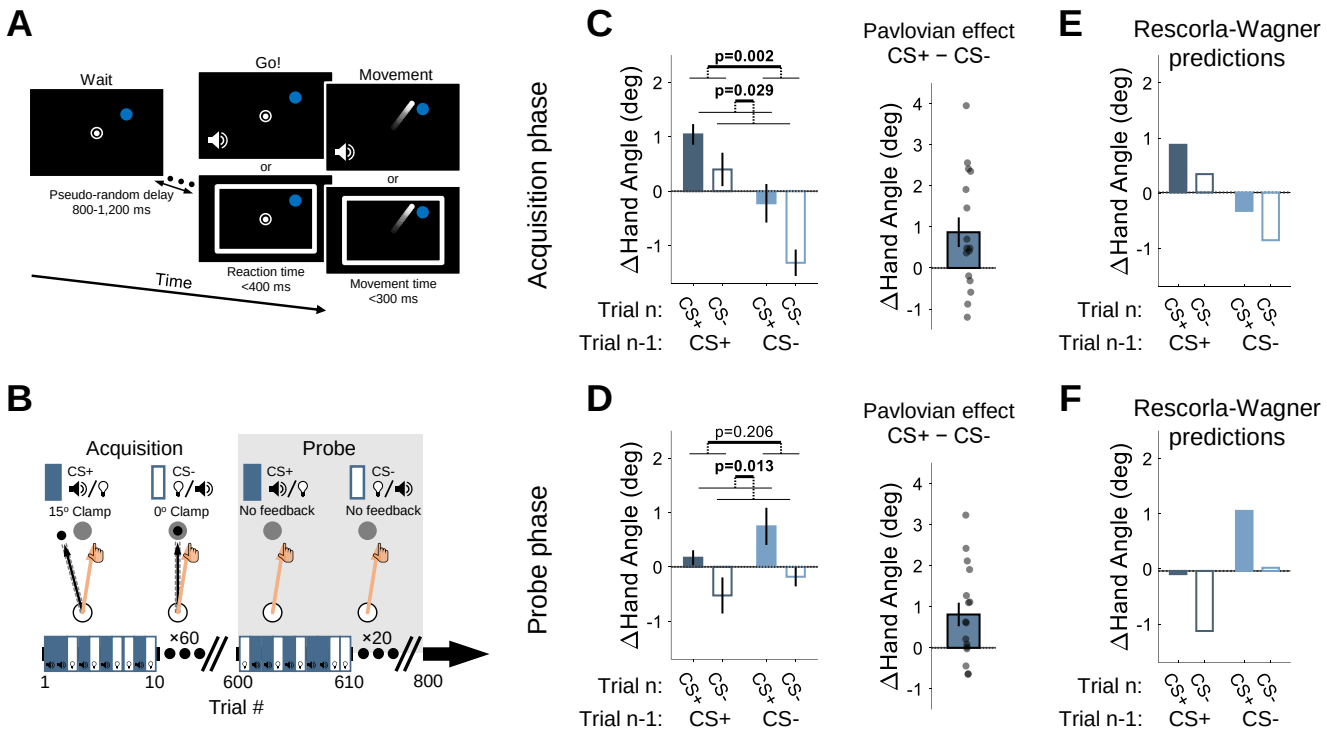

A
Wait
Go!
Movement
or
or
Pseudo-random delay
800-1,200 ms
Reaction time
<400 ms
Movement time
<300 ms
Time
B
Acquisition
Probe
CS+
CS-
15º Clamp
0º Clamp
No feedback
No feedback
×60
×20
1
10
600
610
800
Trial #
Acquisition phase
Probe phase
C
D
E
F
p=0.002
p=0.029
p=0.206
p=0.013
Pavlovian effect
CS+ − CS-
Rescorla-Wagner
predictions
ΔHand Angle (deg)
Trial n:
Trial n-1:
CS+
CS-

Figure 2

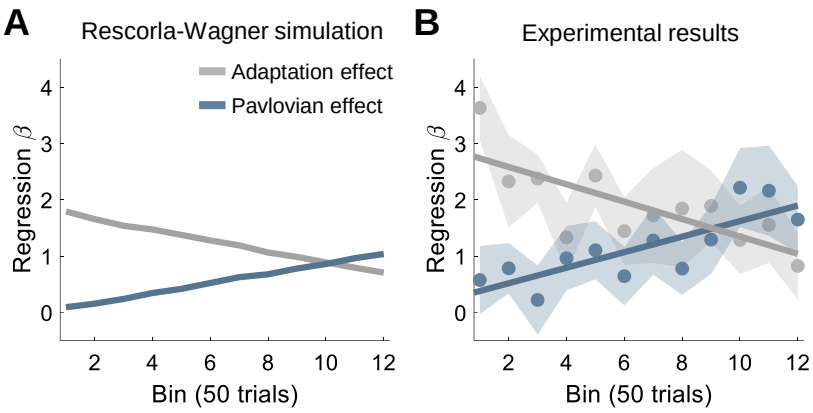
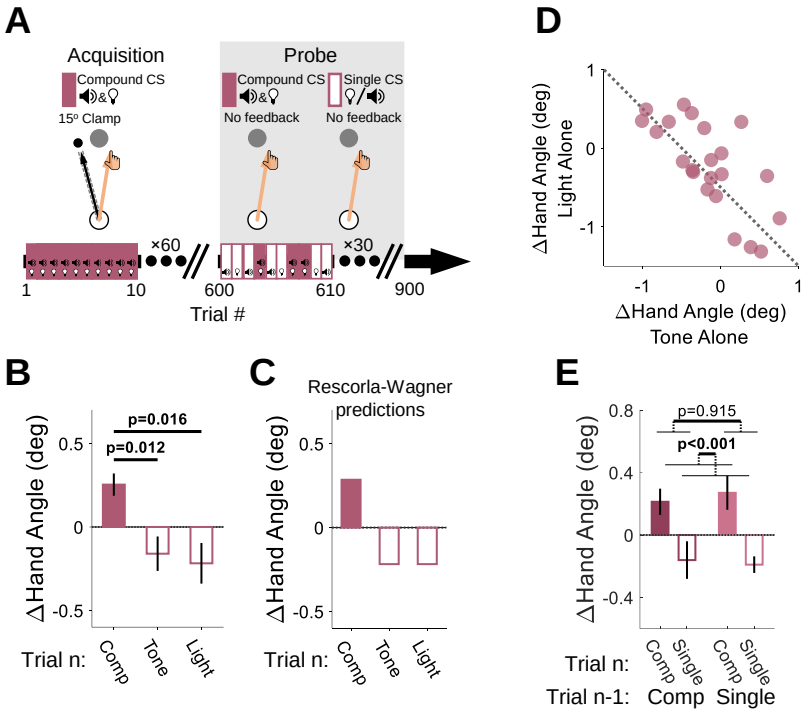

A
Rescorla-Wagner simulation
Adaptation effect
Pavlovian effect
Regression β
Bin (50 trials)
B
Experimental results
Regression β
Bin (50 trials)

Figure 3


A
Acquisition
Compound CS
15º Clamp
Probe
Compound CS
Single CS
No feedback
No feedback
×60
×30
1
10
600
610
900
Trial #
D
ΔHand Angle (deg)
Light Alone
ΔHand Angle (deg)
Tone Alone
B
p=0.016
p=0.012
ΔHand Angle (deg)
Trial n:
Comp
Tone
Light
C
Rescorla-Wagner
predictions
ΔHand Angle (deg)
Trial n:
Comp
Tone
Light
E
p=0.915
p<0.001
ΔHand Angle (deg)
Trial n:
Comp
Single
Comp
Single
Trial n-1:
Comp
Single