Contextual effects in sensorimotor adaptation adhere to associative learning rules

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ABSTRACT

Traditional associative learning tasks focus on the formation of associations between salient events and arbitrary stimuli that predict those events. This is exemplified in cerebellar-dependent delay eyeblink conditioning, where arbitrary cues such as a light or tone act as conditioning stimuli that predict aversive sensations at the cornea. Here we ask if a similar framework could be applied to another type of cerebellar-dependent sensorimotor learning- sensorimotor adaptation. Models of sensorimotor adaptation posit that the introduction of an environmental perturbation results in an error signal that is used to update an internal model of a sensorimotor map for motor planning. Here we take a step towards an integrative account of these two forms of cerebellar-dependent learning, examining the relevance of core concepts from associative learning for sensorimotor adaptation. Using a visuomotor adaptation reaching task, we paired movement-related feedback with neutral auditory or visual contextual 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 contextual effects could not be captured by the conventional algorithms used to describe sensorimotor adaptation. The signature of associative learning effects in sensorimotor adaptation provides a proof-of-concept for linking cerebellar-dependent learning paradigms within a common theoretical framework.

SIGNIFICANCE STATEMENT

Sensorimotor adaptation is a cerebellar-dependent learning 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 demonstrate that core associative learning phenomena observed in studies of eyeblink conditioning are also manifest during sensorimotor adaptation, pointing to a common framework for these distinct cerebellar-dependent motor learning processes.

INTRODUCTION

Sensorimotor adaptation refers to the gradual adjustment of movements in response to changes in the environment or body. In laboratory adaptation tasks, the introduction of perturbed sensory feedback results in a sensorimotor prediction error. This error signal is used to update a model of an internal sensorimotor mapping, thus ensuring that the sensorimotor system remains well-calibrated (Shadmehr and Krakauer, 2008; Wolpert et al., 1995; Wolpert and Ghahramani, 2000). The integrity of the cerebellum is essential for this form of error-based learning (Donchin et al., 2011; Izawa et al., 2012; Popa et al., 2016; Schlerf et al., 2012), and is thought to play a key role in generating predictions of future states given the current sensory context.

Different contexts may call for the use of different sensorimotor mappings. For instance, distinct motor memories should be retrieved when a skilled tennis player prepares to hit a service return on a clay court versus a grass court. A topic of considerable discussion in the adaptation literature centers on the constraints underlying effective contextual cues (Heald et al., 2020; Howard et al., 2013). Contextual cues are highly effective when the cue is directly relevant to properties of the movement. For example, people can simultaneously adapt to opposing sensorimotor perturbations if the context is established by the movement segment that precedes

or follows the perturbed segment of a reach (Howard et al., 2012, 2015; Sheahan et al., 2016). In these situations, the contextual cues are hypothesized to be effective because the cues are incorporated into the motor plan (Howard et al., 2012, 2013).

Less clear is the efficacy of arbitrary contextual cues, ones that are not directly related to movement. In general, arbitrary cues do not appear to be effective for defining distinct motor memories. For example, participants show large interference between opposing perturbations that are signaled by color cues (Howard et al., 2012, 2013; Gandolfo et al., 1996). This interference can be reduced with multiple days of practice, although even after 10 days of training, residual interference remains on trials immediately following a switch in context (Addou et al., 2011; see also Osu et al., 2004).

The ineffectiveness of arbitrary contextual cues in shaping sensorimotor adaptation is surprising when one considers another popular model task of cerebellar-dependent learning – delay eyeblink conditioning. In this form of classical conditioning, a sensory cue (e.g., a tone) is repeatedly paired with an aversive event (e.g., air puff to the cornea). After just a short training period, organisms as diverse as turtles and humans produce an adaptive, conditioned response (e.g., eye blink prior to the aversive event). Notably, there is little constraint on the features of the predictive cues: The conditioned response can be readily acquired in response to arbitrary predictive events, such as a tone or a light flash. In contrast, at least with respect to cerebellar-dependent eyeblink conditioning, there are significant temporal constraints: The cue must appear before the aversive event and the two stimuli must be in close temporal proximity (Schneiderman and Gormezano, 1964; Smith et al., 1969).

In the present study, we set out to re-evaluate the efficacy of arbitrary cues in sensorimotor adaptation, drawing on key theoretical concepts and design features employed in studies of delay eyeblink conditioning. Using a variant of a visuomotor adaptation task, we show that arbitrary stimuli can act as effective contextual cues when a strict temporal relationship is established

between those cues and their associated movement-related sensory outcomes. We then take this phenomenon a step further, demonstrating a direct link between sensorimotor adaptation and eyeblink conditioning by showing that the effect of these arbitrary cues adheres to an established core principle of associative learning – cue additivity. The parallels between adaptation and conditioning observed in our results lay the empirical groundwork for a more parsimonious model of cerebellar-dependent sensorimotor learning.

RESULTS

Our primary goal in the present study was to determine if arbitrary stimuli can serve as effective contextual cues in sensorimotor adaptation. Participants reached from a start location to a target with movement feedback provided by a cursor (Fig. 1A). In typical adaptation tasks, the onset of the target serves as the imperative for movement initiation. Here, the target was always visible at a fixed location, and we used an arbitrary cue – either a tone or light stimulus – as the imperative. When considered through the lens of classical conditioning, the arbitrary cues are the conditioned stimuli (CSs), and the movement feedback is the unconditioned stimulus (US). For optimal delay eyeblink conditioning, the interval between the CS and the US is relatively narrow, on the order of 100-500 ms (Schneiderman and Gormezano, 1964; Smith et al., 1969). By using a neutral stimulus to cue movement initiation, we imposed a tight temporal link between the CS and the US, requiring the participant to initiate the movement within 400 ms of the onset of the imperative. Participants complied with this requirement, exhibiting rapid response times ([Mean ± STD]: 287±45.2 ms).

To elicit adaptation, we perturbed the visual feedback. A common perturbation technique is visuomotor rotation, where the movement path of a visual feedback cursor is rotated (about the origin) with respect to the hand's path. Implicit adaptation causes the heading angle of movements

to shift across trials in the direction opposite the rotated cursor, thus offsetting the error (Krakauer et al., 2000). To continue with the analogy to conditioning, the conditioned response (CR) would be the movement heading angle elicited by a CS, with learning inferred by the change in heading angle across trials following the pairing of that CS with a US. We note that the unconditioned response (UR) in an adaptation task should correspond to an immediate movement correction to the perturbation; that is, an on-line correction. Given that we require fast movements to minimize these corrections, the UR is not observed in our design.

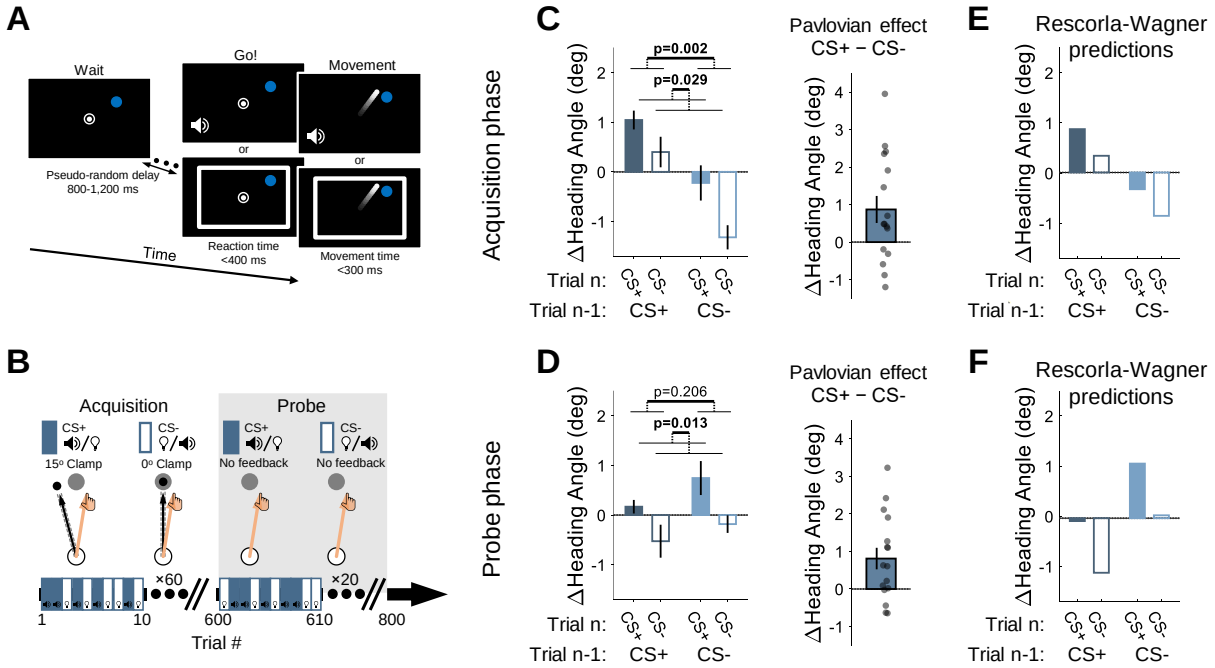

Figure 1. Experiment 1: Differential Conditioning.

(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 path is independent of the hand's path ("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 heading 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 heading 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.

Rather than rotate the position of the feedback cursor with respect to the veridical hand position, we opted to use a visual "clamp" where the cursor followed an invariant path with respect to the target (Morehead et al., 2017; Shmuelof et al., 2012). The participant was fully informed of this manipulation and was instructed to always reach straight to the target and ignore the task-irrelevant cursor. Despite these instructions, participants' reach angles gradually shift in the direction opposite the error clamp, showing all of the cardinal signatures of implicit sensorimotor adaptation (Morehead et al., 2017; Kim et al., 2018; Tsay et al., 2020, 2021; Avraham et al., 2021; Poh et al., 2021; Vandevoorde and Orban de Xivry, 2019; Yin and Wei, 2020). In contrast to traditional movement-contingent feedback, the clamp method eliminates confounding effects that can come about from strategic processes (McDougle et al., 2016; Kim et al., 2020) and the size of the error can be controlled on every trial.

Sensorimotor adaptation is modulated by arbitrary sensory cues

In a standard differential conditioning design, 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 CSs – a tone or a light cue (Figs. 1A, 1B). For the CS+ condition, the feedback cursor followed a clamped

path that was rotated from the target by 15°. Rather than eliminate the US on CS- trials, we used a 0° clamp in which the feedback cursor always moved directly to the target. Thus, there was always a US on each trial, with the 15° US creating an error signal (paired with the CS+) and the 0° US signaling the absence of error (paired with the CS-).

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 single 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 heading angle. The change in heading 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 heading angle), and following no error on CS- trials, decreased adaptation (i.e., extinction). We refer to these trial-by-trial changes as the “adaptation effect”, the standard measure of learning in sensorimotor adaptation tasks. However, the conditioning framework makes a critical additional prediction: The CS+ and CS- should differentially modulate the hand’s heading 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 heading angle between the two cues that is independent of the feedback received on 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.

There was a robust adaptation effect (Fig. 1C, left panel): Trial-by-trial changes in reaching direction (Δ heading 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 heading angle was larger after CS+ trials compared to after CS- trials. That is, the error occurring on CS+ trials resulted in learning

that carried over to the next trial, whereas the absence of an error on a previous CS- trial resulted in a relative reversion to baseline (extinction). This is the canonical signature of incremental sensorimotor 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 heading angle increased in the direction of adaptation on CS+ trials (i.e., a positive change in heading 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 sensorimotor 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 heading angle differences on CS+ and CS- trials could be affected by rapid online feedback corrections. This explanation is unlikely given that the movements were quite rapid ([Mean±STD], 103±31.2 ms). To assess the online correction hypothesis more directly, we calculated the difference in heading angle 50 ms after movement initiation and at the radial distance of the target. There was no overall change in heading 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 heading 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* [$F(1,15)=7.98$, $p=0.013$, $\eta_p^2=0.35$] (Fig. 1D), with a relative increase in heading angle on CS+ trials and a decrease on CS- trials. Moreover, there was neither an effect of the trial *n-1* CS [$F(1,15)=1.74$, $p=0.206$, $\eta_p^2=0.10$] nor a trial *n-1* x *n* interaction [$F(1,15)=0.25$, $p=0.621$, $\eta_p^2=0.02$], consistent with adaptation effects 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 sensorimotor adaptation in both the acquisition and probe phases in Experiment 1 are consistent with differential conditioning effects observed in delay eyeblink conditioning. Feedforward implicit sensorimotor 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 sensorimotor adaptation is based on a “state-space” model in which the motor state is updated according to the error observed during the previous movement. The parameters of this model determine both the trial-by-trial retention of the previous motor state and the rate of learning from errors (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 heading angle is produced by the trial *n* CS; thus, this standard model cannot capture context effects (e.g., the Pavlovian effect).

One influential model that has been used to describe contextual effects in associative learning tasks is the Rescorla-Wagner model (Rescorla and Wagner, 1972). This model 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 $\lambda - V^{[n-1]}$, where λ is the maximum conditioning (asymptotic) level for 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 the error-correction process itself (e.g., the fact that the motor system “knows” to update movements in the direction opposite of the error). For simplicity, we can assume that the sign of the change in movement direction is determined by a specialized neural circuit attempting to reduce 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 demonstrated 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 heading 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 CSs) have no natural relevance for reaching; as such, their contribution to the CR should initially be quite modest, but gradually increase with experience (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 of acquisition, the adaptation effect emerged rapidly

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).

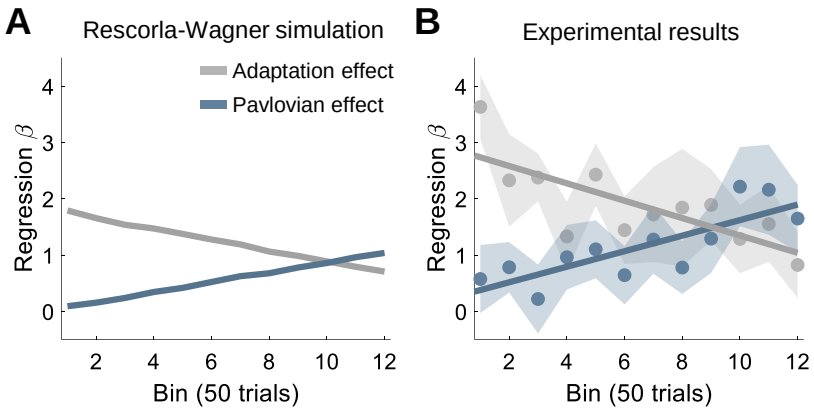

Figure 2. Dynamics of adaptation and Pavlovian effects.

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 regions represent SEM.

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

The differential conditioning results of Experiment 1 show that implicit sensorimotor adaptation manifests a prominent feature of associative learning, the gradual associability of sensorimotor feedback with arbitrary sensory cues. In Experiment 2, we tested another core

feature 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. That is, 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 examine 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. 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 sensorimotor 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 of the acquisition phase. As in Experiment 1, we again observed robust adaptation in the acquisition phase, manifest as a change in heading angle in the direction opposite to the clamp (Fig. S1).

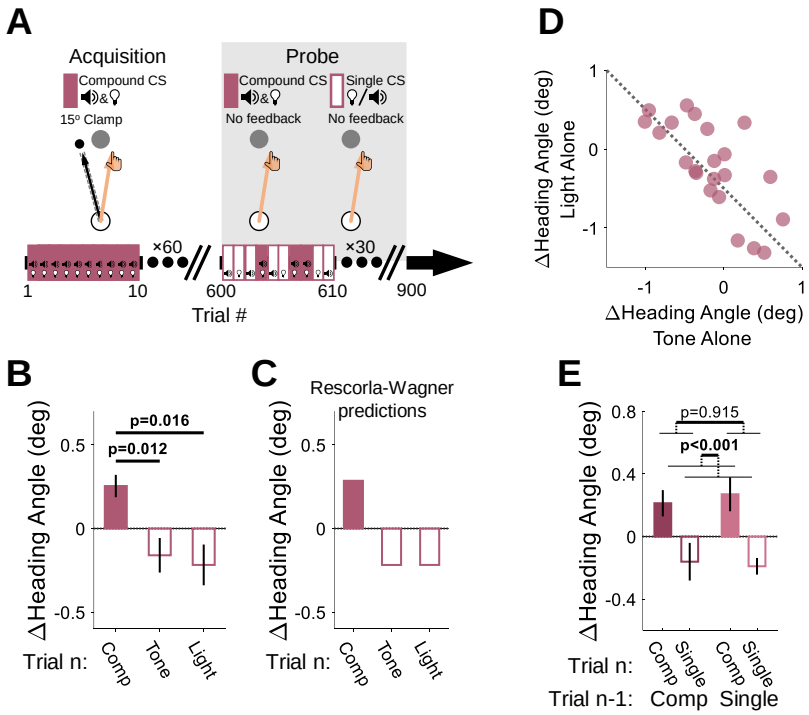

Figure 3. Experiment 2: Compound Conditioning.

(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 heading 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 heading 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 heading 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 presented 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 heading angles 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 on associability (*V*). This prediction was strikingly confirmed in an analysis of the heading 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 itself 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 heading 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 heading angle for the compound CS (Mean ± SE, 0.24°±0.06°) and a relative decrease for the singleton 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 adaptation effects given the absence of visual feedback in the probe phase.

DISCUSSION

Sensorimotor adaptation and delay eyeblink conditioning are foundational paradigms for studying 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 that arise when 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 shaped by arbitrary sensory context cues.

The present study takes a first step toward a more parsimonious framework that can account for these two canonical forms of cerebellar-dependent motor learning. We were motivated by the apparent paradox concerning whether arbitrary stimuli can act as sufficient contextual cues for the establishment of distinct motor memories during sensorimotor adaptation. In attempting to resolve this paradox, we conceptualized adaptation as analogous to an associative learning process. Seen from this perspective, we recognized that prior studies that failed to observe adaptation in response to arbitrary context cues had not considered the rather precise temporal relationship of these cues to the feedback. By modifying a visuomotor adaptation task to conform to timing constraints similar to those required for delay eyeblink conditioning, we showed that 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 (i.e., tones and lights) with distinct visuomotor outcomes can differentially influence implicit feedforward sensorimotor adaptation, and, furthermore, do so in a manner consistent with core principles of associative learning.

The role of context in sensorimotor adaptation has been the subject of considerable debate, with a large body of empirical studies asking whether different sensory cues can be sufficient to “tag” different motor memories. Postural and movement-related variables, such as different lead-in and follow-through movements, are very effective contextual cues, allowing participants to respond to interleaved, opposing perturbations with minimal interference (Howard et al., 2012, 2013, 2015; Sheahan et al., 2016). In contrast, arbitrary visual features, such as color, are generally ineffective (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). To account for this discrepancy, it has been proposed that movement-related cues are dynamically incorporated into the motor state, allowing for the separation of distinct internal models, whereas arbitrary cues are not sufficiently relevant to the motor state (Howard et al., 2012, 2013).

In the current study, we found compelling contextual effects using arbitrary sensory cues. We imposed a strong temporal constraint on the interval between the contextual cues and the feedback by having the cues serve as imperative signals and enforcing rapid response times. This strict temporal constraint was more relaxed in prior studies; for example, in Howard et al. (Howard et al., 2013), a color cue was presented 1,000 ms before the imperative, an interval beyond the window for optimal cerebellar-dependent learning (Brudner et al., 2016; Kitazawa et al., 1995; Schneiderman and Gormezano, 1964; Smith et al., 1969). Second, the salience of the arbitrary cues was likely heightened in the present study by having them serve as movement imperatives, requiring the participants’ attention to the cues.

We note that these temporal constraints and salience requirements are likely built into standard, implicit adaptation tasks in which feedback is perturbed while a participant reaches to a visual target. The target itself is a salient stimulus that defines the task goal and movement plan, and its onset usually serves as the imperative for movement initiation. Under these conditions, the target might be viewed as a highly effective contextual cue. Moreover, RTs in these tasks are

typically below 500 ms (Kim et al., 2019, 2018; Avraham et al., 2021); as such, a tight temporal link is established between target appearance and movement, echoing (perhaps inadvertently) the CS-US temporal constraints essential for delay eyeblink conditioning.

More precisely, we propose that it is the movement plan itself, rather than the target cue, that constitutes the primary CS. 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 behaving like a CS may provide a parsimonious account of several phenomena. First, generalization of adaptation is centered around the direction of the movement plan, not the target (Day et al., 2016; McDougle et al., 2017). This echoes generalization effects seen in eyeblink conditioning, where variations on the learned CS (e.g., altering the tone’s frequency) lead to parametric changes in CR probability (Siegel et al., 1968), showing a similar Gaussian shape as that seen in adaptation generalization. Second, even in the absence of distinct contextual movements (e.g. follow-throughs), the activation of different motor plans can serve as efficient contextual cues, negating interference effects from opposing perturbations (Sheahan et al., 2016, 2018). Third, an emphasis on the movement plan is in accord with theoretical models of cerebellar-dependent adaptation, where the prediction that constitutes the basis for the 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).

Our focus has been on features of sensorimotor adaptation that map onto the CS, US, and the CR. The UR in this context would be an automatic action that is immediately triggered by the US. We assume this would be the on-line correction to a perceived error. While there is a rich literature showing the automatic and relatively fast latency of this corrective response (e.g., around 150 ms, Carroll et al., 2019; Franklin and Wolpert, 2008), we opted to use rapid shooting movements to isolate feedforward adaptation, and thus no reliable feedback corrections were

observed (see *Results*). We recognize that a feedback response potentiated by the perturbation might be utilized for feedforward learning (Albert and Shadmehr, 2016). Alternatively, a UR is not required for conditioning processes arising from volitional behaviors (e.g., Cartoni et al., 2016).

To formally relate eyeblink conditioning and adaptation, 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 trivial 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, a standard state-space model could be modified such that different sensory cues become associated with different independent states (Heald et al., 2018), thus allowing for context-dependent learning (e.g., differential conditioning). However, we emphasize that to account for compound conditioning, and in particular the additivity principle (i.e., overshadowing), a state-space model would essentially have to be transformed into a facsimile of a Rescorla-Wagner model, thus supporting our key conclusions.

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 are not accounted for by the model. 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).

While the Rescorla-Wagner model cannot account for spontaneous recovery and the effects of perturbation consistency, we envision that more sophisticated models inspired by associative learning theory could readily accommodate these effects. For example, associative mechanisms might be accompanied by Bayesian inference processes that carve the world into distinct contexts (Collins and Frank, 2013; Gershman, 2015). Indeed, Heald and colleagues (Heald et al., 2020) recently used this approach to demonstrate how contextual representations in sensorimotor adaptation can allow for the establishment of multiple motor memories, with spontaneous recovery and consistency effects emerging due to contextual inferences.

Motivated by the cerebellar literature, we focused on delay eyeblink conditioning in considering how associative learning mechanisms can account for contextual effects in sensorimotor adaptation. We recognize that conditioning effects can be much more complex than the behavioral changes that arise from the pairing of two stimuli (Rescorla, 1988). These include associations between a CS and an action (Skinner, 1938), learning that does not abide by strict timing requirements (Gallistel and Gibbon, 2000), and other conditioning processes (e.g., trace conditioning) that rely on brain structures other than the cerebellum (Clark et al., 2002; Clark and Squire, 1998). Multiple learning processes allow the organism to build a comprehensive representation of the world, with the ability to flexibly modify behavior at many levels of control in response to changes in the contingencies between the body and environment (McDougle et al., 2016; Kim et al., 2020). Nonetheless, by showing that core constraints of delay eyeblink conditioning are relevant for sensorimotor adaptation, our study may help develop a formal framework for looking at these two domains in a unified manner.

While our results highlight principles that address context-dependent sensorimotor 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 (Wolpert and Ghahramani, 2000; but see Hadjiosif et al., 2021). Associative learning alone does not provide a mechanism for this sign-dependent error correction process (e.g., the directional change of reaching movements given rotated feedback, or the precise timing of an eyeblink response to an air puff). Rather, it describes the association between a contextual cue and a salient event (e.g., shock, reward, etc.). Speculatively, sensorimotor adaptation may operate as a lookup table of context-outcome associations learned by a system designed to keep the sensorimotor system exquisitely calibrated. A model of this form could bring sensorimotor adaptation closer to classical associative models of cerebellar learning and plasticity (Albus, 1971; Ito, 1984; Marr, 1969).

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), 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). In delay eyeblink conditioning, learning is optimal when the US is presented 100 to 500 ms after the CS (Schneiderman and Gormezano, 1964; Smith et al., 1969). To minimize the delay between the onset of the CS and the US (the clamped feedback), 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. Pilot work showed that RTs with the variable imperative onset time were always greater than 100 ms; as such, we did not set a minimum RT bound. 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 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’s angular 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 (heading angle) and the trial-by-trial changes in heading angle (Δ heading angle). heading 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 heading angle was larger than 100° off from the target, or in which the trial-to-trial change in heading 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 heading angle analysis, but not for the presentation of heading 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 heading angle was flipped for participants who experienced a CCW clamp, such that a positive heading angle is in the direction of expected adaptation (i.e., opposite the direction of the perturbed feedback). Moreover, the heading angle on the first acquisition trial was treated as the baseline reaching angle and subtracted from the heading 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 heading 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 heading 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 heading angle was the dependent variable in the two ANOVAs. To examine the dynamics of the adaptation and Pavlovian effects (Fig. 2B), we binned the heading angle data into epochs of 50 trials. Within each bin, we performed multiple regression analysis to test whether trial-to-trial change in heading 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 heading 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 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 heading 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 heading 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 heading 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 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 heading angle between CS+ and CS- trials. In addition, we illustrated that a single-process state-space model, a standard model of sensorimotor adaptation, cannot capture these Pavlovian effects. In this model of sensorimotor 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 (Fig. 2B), we simulated the trial-by-trial change in heading 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 heading angle data (see *Data analysis*) with the exception that the dependent variable was now the simulated change in heading angle.

Model fitting and comparison

We conducted a *post-hoc* model comparison analysis (Fig. S3). In this analysis, we fit the Rescorla-Wagner model (Eqs. 1 and 2) and the standard state-space model (Eq. 3) to participants' heading 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], except for λ, which was bounded at [-30, 60]. We did not perform model fitting for Experiment 2 since all trials were 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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REFERENCES

Addou T, Krouchev N, Kalaska JF. 2011. Colored context cues can facilitate the ability to learn and to switch between multiple dynamical force fields. *Journal of Neurophysiology* **106**:163–183. doi:10.1152/jn.00869.2010

Akaike H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**:716–723. doi:10.1109/TAC.1974.1100705

Albert ST, Jang J, Sheahan HR, Teunissen L, Vandevoorde K, Herzfeld DJ, Shadmehr R. 2021. An implicit memory of errors limits human sensorimotor adaptation. *Nature Human Behaviour* 1–15. doi:10.1038/s41562-020-01036-x

Albert ST, Shadmehr R. 2016. The Neural Feedback Response to Error As a Teaching Signal for the Motor Learning System. *J Neurosci* **36**:4832–4845. doi:10.1523/JNEUROSCI.0159-16.2016

Albus JS. 1971. A theory of cerebellar function. *Mathematical Biosciences* **10**:25–61. doi:10.1016/0025-5564(71)90051-4

Avraham G, Keizman M, Shmuelof L. 2020. Environmental consistency modulation of error sensitivity during motor adaptation is explicitly controlled. *Journal of Neurophysiology* **123**:57–69. doi:10.1152/jn.00080.2019

Avraham G, Morehead JR, Kim HE, Ivry RB. 2021. Reexposure to a sensorimotor perturbation produces opposite effects on explicit and implicit learning processes. *PLOS Biology* **19**:e3001147. doi:10.1371/journal.pbio.3001147

Blakemore S-J, Frith CD, Wolpert DM. 2001. The cerebellum is involved in predicting the sensory consequences of action. *NeuroReport* **12**:1879–1884.

Bond KM, Taylor JA. 2015. Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology* **113**:3836–3849. doi:10.1152/jn.00009.2015

Brainard DH. 1997. The Psychophysics Toolbox. *Spatial Vision* **10**:433–436. doi:10.1163/156856897X00357

Brudner SN, Kethidi N, Graeupner D, Ivry RB, Taylor JA. 2016. Delayed feedback during sensorimotor learning selectively disrupts adaptation but not strategy use. *Journal of Neurophysiology* **115**:1499–1511. doi:10.1152/jn.00066.2015

Carroll TJ, McNamee D, Ingram JN, Wolpert DM. 2019. Rapid Visuomotor Responses Reflect Value-Based Decisions. *J Neurosci* **39**:3906–3920. doi:10.1523/JNEUROSCI.1934-18.2019

Cartoni E, Balleine B, Baldassarre G. 2016. Appetitive Pavlovian-instrumental Transfer: A review. *Neuroscience & Biobehavioral Reviews* **71**:829–848. doi:10.1016/j.neubiorev.2016.09.020

Clark RE, Manns JR, Squire LR. 2002. Classical conditioning, awareness, and brain systems. *Trends in Cognitive Sciences* **6**:524–531. doi:10.1016/S1364-6613(02)02041-7

Clark RE, Squire LR. 1998. Classical Conditioning and Brain Systems: The Role of Awareness. *Science* **280**:77–81. doi:10.1126/science.280.5360.77

Collins AGE, Frank MJ. 2013. Cognitive control over learning: Creating, clustering, and generalizing task-set structure. *Psychological Review* **120**:190–229. doi:10.1037/a0030852

Day KA, Roemmich RT, Taylor JA, Bastian AJ. 2016. Visuomotor Learning Generalizes Around the Intended Movement. *eNeuro* **3**. doi:10.1523/ENEURO.0005-16.2016

Donchin O, Rabe K, Diedrichsen J, Lally N, Schoch B, Gizewski ER, Timmann D. 2011. Cerebellar regions involved in adaptation to force field and visuomotor perturbation. *Journal of Neurophysiology* **107**:134–147. doi:10.1152/jn.00007.2011

Franklin DW, Wolpert DM. 2008. Specificity of Reflex Adaptation for Task-Relevant Variability. *J Neurosci* **28**:14165–14175. doi:10.1523/JNEUROSCI.4406-08.2008

Gallistel CR, Gibbon J. 2000. Time, rate, and conditioning. *Psychological Review* **107**:289–344. doi:10.1037/0033-295X.107.2.289

Gandolfo F, Mussa-Ivaldi FA, Bizzi E. 1996. Motor learning by field approximation. *PNAS* **93**:3843–3846. doi:10.1073/pnas.93.9.3843

Gao Z, Proietti-Onori M, Lin Z, ten Brinke MM, Boele H-J, Potters J-W, Ruigrok TJH, Hoebeek FE, De Zeeuw CI. 2016. Excitatory Cerebellar Nucleocortical Circuit Provides Internal Amplification during Associative Conditioning. *Neuron* **89**:645–657. doi:10.1016/j.neuron.2016.01.008

Garcia J, Koelling RA. 1966. Relation of cue to consequence in avoidance learning. *Psychon Sci* **4**:123–124. doi:10.3758/BF03342209

Gershman SJ. 2015. A Unifying Probabilistic View of Associative Learning. *PLoS Comput Biol* **11**. doi:10.1371/journal.pcbi.1004567

Giurfa M. 2007. Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well. *J Comp Physiol A* **193**:801–824. doi:10.1007/s00359-007-0235-9

Gonzalez Castro LN, Hadjiosif AM, Hemphill MA, Smith MA. 2014. Environmental Consistency Determines the Rate of Motor Adaptation. *Current Biology* **24**:1050–1061. doi:10.1016/j.cub.2014.03.049

Hadjiosif AM, Krakauer JW, Haith AM. 2021. Did we get sensorimotor adaptation wrong? Implicit adaptation as direct policy updating rather than forward-model-based learning. *J Neurosci*. doi:10.1523/JNEUROSCI.2125-20.2021

Heald JB, Ingram JN, Flanagan JR, Wolpert DM. 2018. Multiple motor memories are learned to control different points on a tool. *Nature Human Behaviour* **2**:300–311. doi:10.1038/s41562-018-0324-5

Heald JB, Lengyel M, Wolpert DM. 2020. Contextual inference underlies the learning of sensorimotor repertoires. *bioRxiv* 2020.11.23.394320. doi:10.1101/2020.11.23.394320

Hegele M, Heuer H. 2010. Implicit and explicit components of dual adaptation to visuomotor rotations. *Consciousness and Cognition* **19**:906–917. doi:10.1016/j.concog.2010.05.005

Herzfeld DJ, Kojima Y, Soetedjo R, Shadmehr R. 2018. Encoding of error and learning to correct that error by the Purkinje cells of the cerebellum. *Nature Neuroscience* **21**:736–743. doi:10.1038/s41593-018-0136-y

Herzfeld DJ, Vaswani PA, Marko M, Shadmehr R. 2014. A memory of errors in sensorimotor learning. *Science* 1253138. doi:10.1126/science.1253138

Howard IS, Ingram JN, Franklin DW, Wolpert DM. 2012. Gone in 0.6 Seconds: The Encoding of Motor Memories Depends on Recent Sensorimotor States. *J Neurosci* **32**:12756–12768. doi:10.1523/JNEUROSCI.5909-11.2012

Howard IS, Wolpert DM, Franklin DW. 2015. The Value of the Follow-Through Derives from Motor Learning Depending on Future Actions. *Current Biology* **25**:397–401. doi:10.1016/j.cub.2014.12.037

Howard IS, Wolpert DM, Franklin DW. 2013. The effect of contextual cues on the encoding of motor memories. *Journal of Neurophysiology* **109**:2632–2644. doi:10.1152/jn.00773.2012

Hutter SA, Taylor JA. 2018. Relative sensitivity of explicit reaiming and implicit motor adaptation. *Journal of Neurophysiology* **120**:2640–2648. doi:10.1152/jn.00283.2018

Ito M. 1984. The Cerebellum and Neural Control. Raven Press.

Izawa J, Criscimagna-Hemminger SE, Shadmehr R. 2012. Cerebellar Contributions to Reach Adaptation and Learning Sensory Consequences of Action. *J Neurosci* **32**:4230–4239. doi:10.1523/JNEUROSCI.6353-11.2012

Karniel A, Mussa-Ivaldi FA. 2002. Does the motor control system use multiple models and context switching to cope with a variable environment? *Exp Brain Res* **143**:520–524. doi:10.1007/s00221-002-1054-4

Kass RE, Raftery AE. 1995. Bayes Factors. *Journal of the American Statistical Association* **90**:773–795. doi:10.1080/01621459.1995.10476572

Kawato M, Gomi H. 1992. A computational model of four regions of the cerebellum based on feedback-error learning. *Biol Cybern* **68**:95–103. doi:10.1007/BF00201431

Kehoe EJ, Horne AJ, Horne PS, Macrae M. 1994. Summation and configuration between and within sensory modalities in classical conditioning of the rabbit. *Animal Learning & Behavior* **22**:19–26. doi:10.3758/BF03199952

Kehoe EJ, Schreurs BG. 1986. Compound conditioning of the rabbit's nictitating membrane response: Test trial manipulations. *Bull Psychon Soc* **24**:79–81. doi:10.3758/BF03330509

Kim HE, Avraham G, Ivry RB. 2020. The Psychology of Reaching: Action Selection, Movement Implementation, and Sensorimotor Learning. *Annu Rev Psychol*. doi:10.1146/annurev-psych-010419-051053

Kim HE, Morehead JR, Parvin DE, Moazzezi R, Ivry RB. 2018. Invariant errors reveal limitations in motor correction rather than constraints on error sensitivity. *Communications Biology* **1**:19. doi:10.1038/s42003-018-0021-y

Kim HE, Parvin DE, Ivry RB. 2019. The influence of task outcome on implicit motor learning. *eLife* **8**:e39882. doi:10.7554/eLife.39882

Kitazawa S, Kohno T, Uka T. 1995. Effects of delayed visual information on the rate and amount of prism adaptation in the human. *J Neurosci* **15**:7644–7652. doi:10.1523/JNEUROSCI.15-11-07644.1995

Krakauer JW, Hadjiosif AM, Xu J, Wong AL, Haith AM. 2019. Motor LearningComprehensive Physiology. American Cancer Society. pp. 613–663. doi:10.1002/cphy.c170043

Krakauer JW, Pine ZM, Ghilardi M-F, Ghez C. 2000. Learning of Visuomotor Transformations for Vectorial Planning of Reaching Trajectories. *J Neurosci* **20**:8916–8924. doi:10.1523/JNEUROSCI.20-23-08916.2000

Krouchev NI, Kalaska JF. 2003. Context-Dependent Anticipation of Different Task Dynamics: Rapid Recall of Appropriate Motor Skills Using Visual Cues. *Journal of Neurophysiology* **89**:1165–1175. doi:10.1152/jn.00779.2002

Lilliefors HW. 1967. On the Kolmogorov-Smirnov Test for Normality with Mean and Variance Unknown. *Journal of the American Statistical Association* **62**:399–402. doi:10.1080/01621459.1967.10482916

Mackintosh NJ. 1976. Overshadowing and stimulus intensity. *Animal Learning & Behavior* **4**:186–192. doi:10.3758/BF03214033

Marr D. 1969. A theory of cerebellar cortex. *The Journal of Physiology* **202**:437–470. doi:10.1113/jphysiol.1969.sp008820

McDougle SD, Bond KM, Taylor JA. 2017. Implications of plan-based generalization in sensorimotor adaptation. *Journal of Neurophysiology* **118**:383–393. doi:10.1152/jn.00974.2016

McDougle SD, Bond KM, Taylor JA. 2015. Explicit and Implicit Processes Constitute the Fast and Slow Processes of Sensorimotor Learning. *J Neurosci* **35**:9568–9579. doi:10.1523/JNEUROSCI.5061-14.2015

McDougle SD, Ivry RB, Taylor JA. 2016. Taking Aim at the Cognitive Side of Learning in Sensorimotor Adaptation Tasks. *Trends in Cognitive Sciences* **20**:535–544. doi:10.1016/j.tics.2016.05.002

Morehead JR, Taylor JA, Parvin DE, Ivry RB. 2017. Characteristics of Implicit Sensorimotor Adaptation Revealed by Task-irrelevant Clamped Feedback. *Journal of Cognitive Neuroscience* **29**:1061–1074. doi:10.1162/jocn_a_01108

Osu R, Hirai S, Yoshioka T, Kawato M. 2004. Random presentation enables subjects to adapt to two opposing forces on the hand. *Nature Neuroscience* **7**:111–112. doi:10.1038/nn1184

Pavlov IP. 1927. Conditioned reflexes, translated by GV Anrep. *London: Oxford*.

Poh E, Al-Fawakari N, Tam R, Taylor JA, McDougle SD. 2021. Generalization of motor learning in psychological space. *bioRxiv* 2021.02.09.430542. doi:10.1101/2021.02.09.430542

Popa LS, Streng ML, Hewitt AL, Ebner TJ. 2016. The Errors of Our Ways: Understanding Error Representations in Cerebellar-Dependent Motor Learning. *Cerebellum* **15**:93–103. doi:10.1007/s12311-015-0685-5

Rescorla R, Wagner A. 1972. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. *Classical conditioning II: Current research and theory* **2**:64–69.

Rescorla RA. 1988. Pavlovian conditioning: It's not what you think it is. *American Psychologist* **43**:151–160. doi:10.1037/0003-066X.43.3.151

Schlerf JE, Ivry RB, Diedrichsen J. 2012. Encoding of Sensory Prediction Errors in the Human Cerebellum. *J Neurosci* **32**:4913–4922. doi:10.1523/JNEUROSCI.4504-11.2012

Schneiderman N, Gormezano I. 1964. Conditioning of the nictitating membrane of the rabbit as a function of CS-US interval. *Journal of Comparative and Physiological Psychology* **57**:188–195. doi:10.1037/h0043419

Shadmehr R, Krakauer JW. 2008. A computational neuroanatomy for motor control. *Exp Brain Res* **185**:359–381. doi:10.1007/s00221-008-1280-5

Sheahan HR, Franklin DW, Wolpert DM. 2016. Motor Planning, Not Execution, Separates Motor Memories. *Neuron* **92**:773–779. doi:10.1016/j.neuron.2016.10.017

Sheahan HR, Ingram JN, Žalalytė GM, Wolpert DM. 2018. Imagery of movements immediately following performance allows learning of motor skills that interfere. *Scientific Reports* **8**:14330. doi:10.1038/s41598-018-32606-9

Shmuelof L, Huang VS, Haith AM, Delnicki RJ, Mazzoni P, Krakauer JW. 2012. Overcoming Motor "Forgetting" Through Reinforcement Of Learned Actions. *J Neurosci* **32**:14617–14621a. doi:10.1523/JNEUROSCI.2184-12.2012

Siegel S, Hearst E, George N. 1968. Generalization gradients obtained from individual subjects following classical conditioning. *Journal of Experimental Psychology* **78**:171–174. doi:10.1037/h0026178

Skinner BF. 1938. The behavior of organisms: an experimental analysis, The behavior of organisms: an experimental analysis. Oxford, England: Appleton-Century.

Smith MA, Ghazizadeh A, Shadmehr R. 2006. Interacting Adaptive Processes with Different Timescales Underlie Short-Term Motor Learning. *PLOS Biology* **4**:e179. doi:10.1371/journal.pbio.0040179

Smith MC, Coleman SR, Gormezano I. 1969. Classical conditioning of the rabbit's nictitating membrane response at backward, simultaneous, and forward CS-US intervals. *Journal of Comparative and Physiological Psychology* **69**:226–231. doi:10.1037/h0028212

Taylor JA, Krakauer JW, Ivry RB. 2014. Explicit and Implicit Contributions to Learning in a Sensorimotor Adaptation Task. *J Neurosci* **34**:3023–3032. doi:10.1523/JNEUROSCI.3619-13.2014

Tsay JS, Avraham G, Kim HE, Parvin DE, Wang Z, Ivry RB. 2020. The effect of visual uncertainty on implicit motor adaptation. *Journal of Neurophysiology* **125**:12–22. doi:10.1152/jn.00493.2020

Tsay JS, Ivry RB, Lee A, Avraham G. 2021. Moving outside the lab: The viability of conducting sensorimotor learning studies online. *NBDT* **5**:1–22. doi:10.51628/001c.26985

Vandevoorde K, Orban de Xivry J-J. 2019. Internal model recalibration does not deteriorate with age while motor adaptation does. *Neurobiology of Aging* **80**:138–153. doi:10.1016/j.neurobiolaging.2019.03.020

Weiss SJ. 1972. Stimulus compounding in free-operant and classical conditioning: A review and analysis. *Psychological Bulletin* **78**:189–208. doi:10.1037/h0032956

Wolpert DM, Flanagan JR. 2001. Motor prediction. *Current Biology* **11**:R729–R732. doi:10.1016/S0960-9822(01)00432-8

Wolpert DM, Ghahramani Z. 2000. Computational principles of movement neuroscience. *Nature Neuroscience* **3**:1212–1217. doi:10.1038/81497

Wolpert DM, Ghahramani Z, Jordan MI. 1995. An internal model for sensorimotor integration. *Science* **269**:1880–1882. doi:10.1126/science.7569931

Wolpert DM, Miall RC, Kawato M. 1998. Internal models in the cerebellum. *Trends in Cognitive Sciences* **2**:338–347. doi:10.1016/S1364-6613(98)01221-2

Yin C, Wei K. 2020. Savings in sensorimotor adaptation without an explicit strategy. *Journal of Neurophysiology* **123**:1180–1192. doi:10.1152/jn.00524.2019

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 path is independent of the hand's path ("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 heading 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 heading 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 regions 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 heading 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 heading 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 heading 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

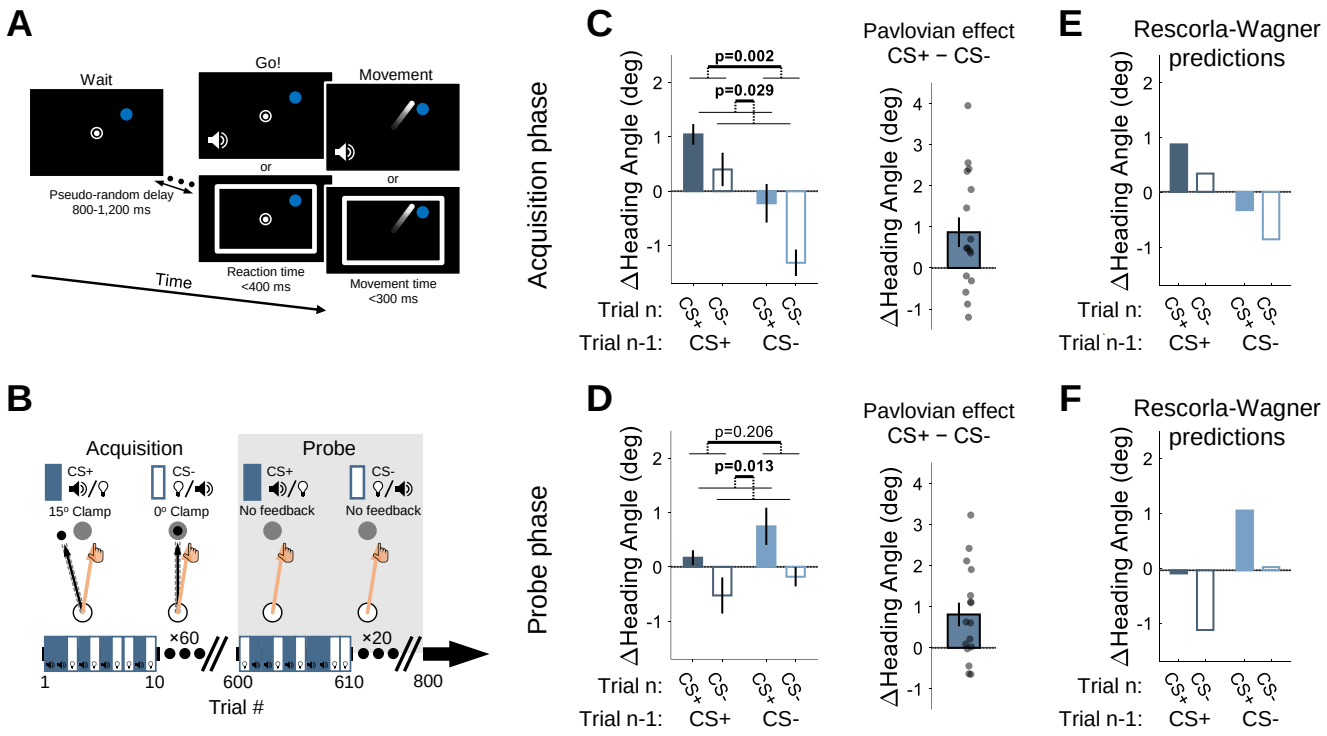

A
Wait
Go!
Movement
or
or
Pseudo-random delay
800-1,200 ms
Reaction time
<400 ms
Movement time
<300 ms
Time
B
Acquisition
Probe
CS+
CS-
15º Clamp
0º Clamp
No feedback
No feedback
×60
×20
1
10
600
610
800
Trial #
Acquisition phase
Probe phase
C
D
p=0.002
p=0.029
p=0.206
p=0.013
ΔHeading Angle (deg)
Trial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

Figure 2

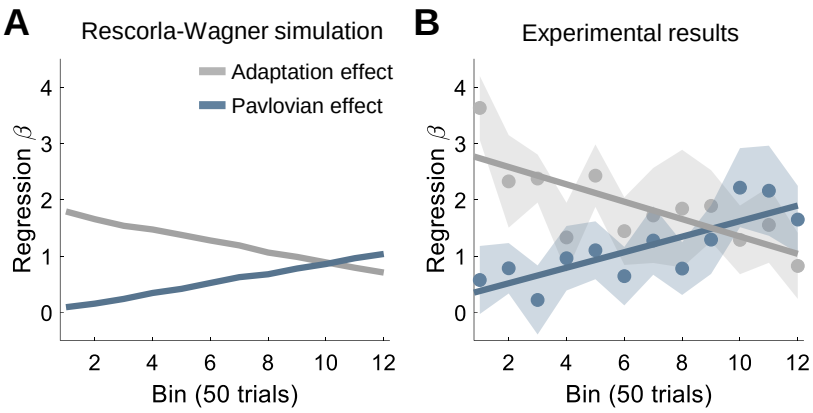
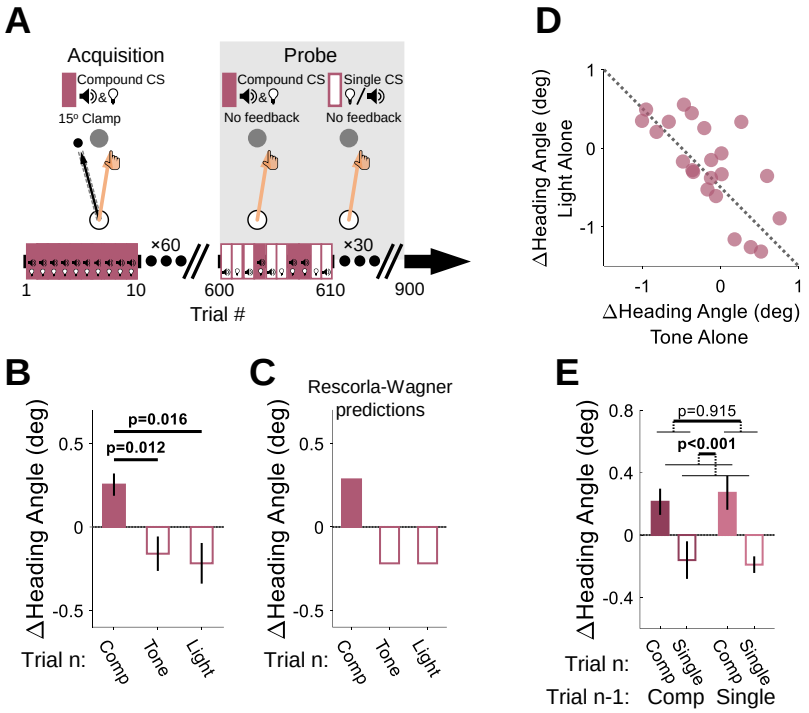

A
Rescorla-Wagner simulation
Adaptation effect
Pavlovian effect
Regression β
Bin (50 trials)
B
Experimental results
Regression β
Bin (50 trials)

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 #
B
p=0.016
p=0.012
ΔHeading Angle (deg)
0.5
0
-0.5
Trial n:
Comp
Tone
Light
C
Rescorla-Wagner predictions
ΔHeading Angle (deg)
0.5
0
-0.5
Trial n:
Comp
Tone
Light
D
ΔHeading Angle (deg) Light Alone
1
0
-1
-1
0
1
ΔHeading Angle (deg) Tone Alone
E
p=0.915
p<0.001
ΔHeading Angle (deg)
0.8
0.4
0
-0.4
Trial n:
Comp
Single
Comp
Single
Trial n-1:
Comp
Single