

Benchmarks for Associative Learning Models

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Abstract

Associative learning, like many mature fields of psychology, is endowed with a nearly unfathomable wealth of empirical data. These arise from multiple experimental procedures and animal species. To assess any proposed theory of associative learning, decisions must be made about which behavioral phenomena to account for. However, there is currently no systematic approach to prioritize observations within this body of evidence. Here, we propose a set of benchmarks that theories should explain: phenomena that are robust across experiments, generalize across procedural variations, and occur under broad but clearly specified circumstances. We queried the expert community for phenomena to be included, reviewed the relevant literature, graded the phenomena into four categories of robustness and generality, and compared our gradings with a second survey of the expert community. We identified 94 benchmark phenomena, of which 16 are domain- and species-general and hence should be explained by any theory claiming generality, and 30 are species- and/or domain-specific but highly robust across procedures. Strikingly, some textbook phenomena that have motivated influential and general associative learning theories are not among these. The remaining 48 phenomena were either tied to particular experimental procedures or of inconclusive generality. Some of their boundary conditions appear to be informally known across laboratories but rarely investigated in a systematic manner. Thus, our review provides a comprehensive evaluation of the current evidence, which will direct theorizing towards high-priority phenomena while also re-focusing research into areas in which evidence is lacking.

Introduction

Learning statistical associations between events in the environment is considered a fundamental ability across many animal taxa including humans. A century of research, going back to the seminal work of Edward Thorndike (1898) and Ivan Pavlov (1927), has generated a nearly unfathomable body of evidence: as of September 2025, *OpenAlex* lists 12,000 and *GoogleScholar* 331,000 articles under the search term “associative learning”. While precise definitions vary, associative learning is broadly understood as a change in behavior resulting from a regularity in the co-occurrence of cues and outcomes (Mackintosh, 1974; Pearce, 2008). These outcomes might appear independent of an agent’s actions (often termed classical or Pavlovian learning), or only after a certain action is emitted by the agent (often termed instrumental learning). In both cases, learning is typically inferred from an increased (or decreased) probability of emitting a response – either one of a range of stereotypical Pavlovian conditioned responses (CR), or the instrumental action that triggers the outcome.

Conceptual theories of associative learning generally propose that this constitutes a basic building block of cognition, from which more complex behaviors are built (Dickinson, 2012). Moreover, clinical conditions such as anxiety and stress-related disorders, substance use disorder, gambling disorder, and even psychosis, have been proposed to result from maladaptive associative learning (Beckers et al., 2023; Gueguen et al., 2021; Suzuki & Kosaki, 2024). All of this lends high relevance to understanding the psychological and neurobiological mechanisms that underlie associative learning.

Yet, there is considerable disagreement about what these mechanisms are, and various conceptual, mathematical, and computational models of associative learning co-exist (Colwill et al., 2022). Crucially, different theories often seek to explain at least partially divergent sets of behavioral phenomena. For example, theories based on discrete

trials do not seek to explain the effect of varying the inter trial interval (ITI), while theories based on continuous time often treat this as a matter of critical importance. Similarly, theories that represent stimuli as discrete entities without graded sensory properties do not seek to explain generalization phenomena. The sheer range of phenomena reported means that it would be a near-endless endeavor to ascertain whether a theory could explain all of the vast number of observations in this field. Indeed, any existing or conceivable theory is probably contradicted by a large number of observations reported in the literature. Moreover, the value of such an exercise would be questionable, as many of these observations have been made only in specific experiments, laboratories, experimental procedures, or species.

In an attempt to bring some structure into this vast space of observations, in 2012 an article identified 86 canonical phenomena, i.e., data patterns repeatedly observed across experiments (Alonso & Schmajuk, 2012). On closer examination, however, these phenomena were of varying credibility and generality. Whereas some had been observed in hundreds if not thousands of experiments around the world and were meticulously dissected in comprehensive reviews, others had been demonstrated only in 2-3 experiments within the same laboratory. Furthermore, existing reviews of one phenomenon typically do not relate to reviews of other phenomena, such that direct comparison between phenomena in terms of their generality and relevance is lacking. In sum, currently the choice of which phenomena to focus on is ad-hoc, or based on researchers' intuition.

To address this prioritization challenge, in the present article we seek to address a fundamental question for which there is currently no unambiguous answer, namely, what are the relevant phenomena that a general theory of associative learning should seek to explain? Here, we define *a phenomenon* as a repeatedly observed data pattern in a clearly

specified procedure. We define *a benchmark* as a phenomenon that is sufficiently robust and generalizable (we will define these two properties in more detail below) to merit evaluating any theory in the field in terms of whether it is consistent with it.

Previous work has addressed a similar question in the field of human working memory (Oberauer et al., 2018). Oberauer and colleagues assumed that not all benchmarks are equally robust and that credible benchmarks are not necessarily equally general, and thus prioritized the benchmarks. To do so, they formed an expert panel to decide on which phenomena to include and graded them into three discrete categories (A-C) of robustness and generality. A motivating justification for this expert approach is that the literature about many phenomena is too heterogenous or too vast (or both) to afford a formal meta-analysis, or even a systematic review, of all phenomena. Oberauer and colleagues conducted an initial online survey to solicit candidate phenomena, in an attempt to minimize bias towards particular theories or observations. After concluding their work, they compared the panel gradings against an expert survey.

Our article follows the same general approach while accounting for the structural differences between the research fields. First, while Oberauer et al. (2018) focused on human working memory, the field of associative learning spans many animal taxa, from invertebrates all the way to humans. Differences between these species have been observed at multiple levels, and the mechanisms of associative learning in snails might not be the same as in rabbits, which in turn might differ from humans. Hence, we considered generality not only in terms of procedural variations, but also in terms of species. To accommodate these multiple factors, we included a fourth and highest grading category AA, in which benchmarks are not only very robust and observed across procedures, but also observed across multiple species, thereby potentially providing information on basic learning principles across the animal kingdom. At the same time,

benchmarks with lower grades, even if very robust and generalizable within species, might not occur in other species, and hence might be addressed by species-specific theories. Thus, we formulated 4 grading categories (AA, A, B, C – see Table 1 for the definition of these categories). Second, we sought to formulate benchmarks in as theory-neutral a manner as possible. Here, the caveat is that the experimental conditions devised to observe certain benchmarks, as well as the appropriate controls, can only be understood in their historical context, which is often shaped by theories prevailing at the time of their discovery. This is why we sometimes describe the theoretical background of particular experimental preparations.

Table 1: Grading system

Grade	Definition
AA	demonstrated across laboratories, highly general across species, reinforcement categories, and conditioned responses
A	demonstrated across laboratories, highly general within species, reinforcement categories, or conditioned responses, and demonstrated in at least one non-human species
B	demonstrated across laboratories, but - procedure-specific AND/OR - specific to humans
C	Credibly demonstrated several times, but - demonstrated within a laboratory but not across AND/OR - highly specific to procedural details AND/OR - considerable rate of null/opposing findings without clear knowledge of boundary conditions

Methods

Procedure

From October 2021 until February 2022, two of the authors (DRB and TB) invited 43 further experts to join an online workshop that took place in May 2022 with the aim of forming a collaborative review consortium. We invited experts who represent the full diversity in the field with respect to investigated species, focus on theory vs. experimentation, areas of expertise, researcher age, gender, seniority, and geographical

region. 27 individuals participated in the workshop, and 14 of these finally joined the consortium. In preparation for the workshop, we conducted an initial anonymous expert survey and asked all workshop participants to list phenomena they considered important enough to discuss. At the workshop, we split the full set of phenomena into 7 work groups, which recruited 6 further experts to share the workload, and met asynchronously to review the relevant literature and draft mini-reviews of each included phenomenon, as well as propose a decision on inclusion as a benchmark and grading. Finally, all work groups met for a concluding workshop in September 2024, in which the inclusion and grading proposals by the working groups were discussed and agreed upon by consensus.

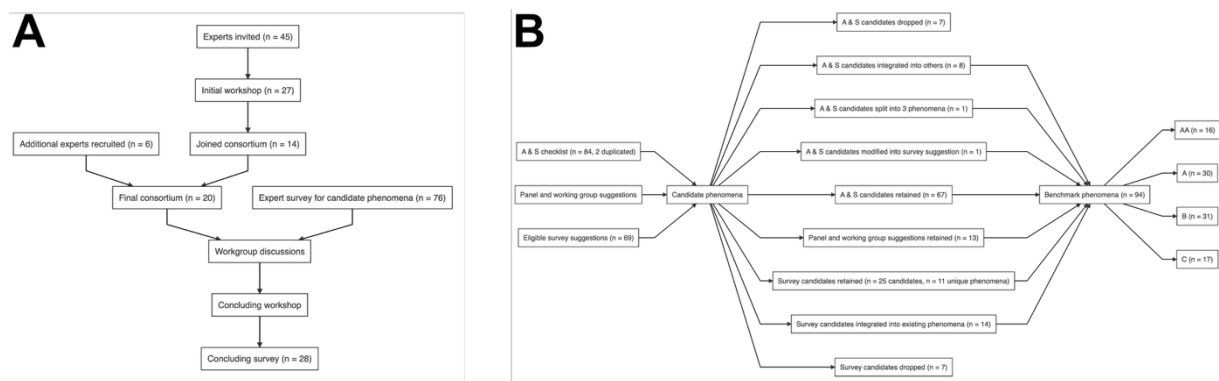


Figure 1. Flowchart of the benchmarking procedure. A. Grading panel and surveyed experts. B. Pathway of candidate phenomena.

Data sources and inclusion criteria

For inclusion of candidate phenomena, we considered three data sources (figure 1B). The first was the checklist by Alonso and Schmajuk (2012), henceforth termed *AS checklist*, comprising 86 phenomena (two of which are duplicates). As this was the initial data source, Table S1 in the supplementary material shows which phenomena from the AS checklist were included in our final list of phenomena. The second source was suggestions by the workshop invitees and consortium participants. We explicitly asked all invitees to suggest important phenomena and considered these regardless of the

proposers' later participation. Finally, we conducted an online survey to address a wider expert community (see below).

Suggested phenomena were considered if they fulfilled two criteria. First, they had to relate to behavioral changes after a conjunction of external events in the environment, and possibly applicable to the conjunction between external events and responses (i.e., instrumental learning), but not by design constrained to instrumental learning. In consequence, instrumental learning phenomena were included only if they involved discriminative cues, since these cues function in an analogous way to the CS in classical conditioning. As an example of an excluded instrumental conditioning phenomenon, superstitious behavior – a wrong solution to the credit assignment problem (Staddon & Zhang, 1991) – does not involve a relation of cues and outcomes, only of several different actions and outcomes. As such, it had no equivalent in classical conditioning and was thus excluded here.

As a second criterion, we required that the experimental manipulation (independent variable) was not necessarily constrained to a particular species (e.g., humans), although the nature of the recorded CR (dependent variable) might be species-specific. Specifically, we stipulated that an experimental manipulation should not necessarily require language, while we admitted CR based on language in humans. An example of an excluded phenomenon is verbally instructed conditioning.

Initial and final survey

The anonymous online surveys were advertised among the participants' laboratories, professional networks, and via mailing lists (including European human fear conditioning researchers, $N = 158$; Australian Learning Group, $N = 252$). We deliberately did not solicit any personal or demographic information in the survey to minimize the

possibility of identification of respondents. The survey instruments and the responses and results are available on OSF (<https://osf.io/fmzh8>).

In the initial survey, implemented in RedCap (P. A. Harris et al., 2009), respondents were asked to “suggest up to 10 phenomena that any associative learning theory should explain”. Between January and March 2022, 76 individuals entered at least one phenomenon into the survey and proposed on average (\pm standard deviation) 7.2 (\pm 3.2) phenomena, resulting in 547 entries overall, of which 297 were string-unique (i.e., with exact duplicates removed). These were initially categorized by one rater (DRB) as either included or not included in the AS checklist. For a subset of survey entries, the initial categorization was cross-checked by additional raters. All novel phenomena and those with uncertain initial categorization were discussed among four of the authors (DRB, TB, DD, RM).

Out of the 297 unique survey responses, 170 referred to one or several phenomena in the AS checklist, 56 did not refer to a phenomenon at all (e.g., they referred to procedures or theoretical concepts), 23 were considered out of scope (e.g., restricted to instrumental conditioning or to humans), and 7 were considered phenomena not sufficiently supported in the literature yet to warrant inclusion. Of the remaining entries, 27 were considered eligible and resulted in the inclusion of 11 new phenomena, and 14 were discussed within the mini-reviews of existing phenomena.

In the final survey, implemented in Qualtrics (Provo, UT, USA), respondents were asked to rate the phenomena by the grades summarized in Table 1. First, we asked them to state how many years of research experience they had in the field of associative learning, and with which species they mostly worked. Because we assumed respondents' expertise would vary considerably, and that at least some respondents would not score the entire phenomena list, we then asked them to order the phenomena categories from

Table 2 in terms of their own expertise. They were then shown these categories in their chosen order. Within each category, all phenomena from Table 2 were listed in randomized order. Respondents were asked to select one of the gradings from Table 1, or one of: “not replicated, or replication yields weak evidence” (D), “I’m familiar with this phenomenon but I’m unsure about the grading” (U), or “This phenomenon is not within my area of expertise” (N). A reminder of what the gradings mean could be invoked as a pop-up window at any time. Respondents could also provide justification for their grading in a free-text field.

Between May and June 2025, $N = 28$ individuals rated at least one phenomenon in the survey and rated 10 - 94 (median: 46) phenomena. Of these experts, 21 indicated they had research experience with humans, 20 with rats, 8 with mice, 1 with rabbits, 8 with pigeons, 1 with corvids, and 3 with invertebrates; 17 had experience with more than one species. Experts indicated 1 - 61 (median: 25) years of research experience in associative learning. Ratings are integrated into Table 2. We considered responses AA-D to compute the grading distribution and median grading. In general, the survey grading distribution overlapped with our grading, and the median survey grading coincided with our grading (35/94) or with an adjacent grade (45/94). The 14 instances of larger deviations are discussed in the results. No phenomenon received a median grading of D, thus supporting our inclusion into the final list.

Terminology

We generally use the term *conditioned stimulus* (abbreviated CS, and denoted by capital letters A, B, C, X, ..., if there is more than one) to refer to different cues in the environment. These are the cues that directly predict the presence or absence of an outcome (Pavlovian conditioning) or the discriminant cues that predict the availability or effectiveness of a certain action that then leads to an outcome (instrumental

conditioning). We use the term *context* to refer to a constellation of discrete cues in the environment (often also denoted with capital letters A, B, C, ... if there is more than one). We use the term *unconditioned stimulus* (abbreviated US, and denoted with US1, US2, ..., if there is more than one), to refer to outcomes. We use the term *conditioned response* (abbreviated CR, and denoted CR1, CR2, ..., when there is more than one CR) to refer to the stereotypical Pavlovian response to the CS, and, for simplicity, also to refer to the instrumental action that triggers the outcome in the case of instrumental learning.

Table 2. Benchmarks graded AA by the panel.

Number	Phenomenon	Description	Source		Survey grading						
					Median	AA	A	B	C	D	n
	Acquisition										
1.1	Acquisition	After a number of CS–US pairings, the CS elicits a conditioned response (CR) that corresponds to a consistent increase or decrease in magnitude or frequency of an observable behaviour.	Alonso & Schmajuk	1.1	AA	19	0	0	0	0	19
1.2	Benefit of spatiotemporal contiguity	CRs are stronger when CS and US are presented close in space and time.	Survey suggestion		AA	12	8	1	0	0	21
1.3	Interstimulus interval (ISI) effects	Strongest CR with relatively short ISIs.	Alonso & Schmajuk	12.1	A	4	6	4	0	0	14
1.4	Second-order conditioning	When A–US pairings are followed by B–A pairings, presentation of B generates a CR.	Alonso & Schmajuk	11.2–11.3	A	6	5	8	1	0	20
1.5	Recency effect	After acquisition, CRs are stronger when the test is closer in time to acquisition.	Survey suggestion		A	3	5	5	1	1	15
1.6	Post-training US revaluation	After CS-US pairings, revaluation of the US affects the response to the CS.	Survey suggestion		A	7	6	3	3	0	19
	Generalisation										
2.1	Generalisation	A novel cue elicits a CR to the degree that it shares some characteristics with a CS that has been paired with the US.	Alonso & Schmajuk	3.1	AA	7	2	1	0	0	10
2.2	Peak & area shift	After intradimensional discrimination training, generalisation gradients increase beyond the CS+ in the opposite direction from the CS-.	Survey suggestion & expert suggestion		A	2	3	2	0	1	8
	Discrimination										
3.1	Differential/discriminative training	After receiving training in which one CS is followed by a US (CS+) and another CS is not followed by a US (CS-), the difference in responding to the two stimuli is greater than if only CS+ were trained and CS- first encountered at test.	Alonso & Schmajuk	4.1	AA	4	3	0	0	0	7
3.2	Positive patterning	After training with intermixed presentations of a compound of two stimuli followed by an outcome (AB+) and each of the individual stimuli followed by no outcome (A- / B-), responding to the compound is stronger than responding to the individual stimuli.	Alonso & Schmajuk	4.2	AA	5	5	0	0	0	10
3.3	Asymmetry in intensity/magnitude discrimination	When a discrimination (A+, B-) involves stimuli that differ in intensity or magnitude, acquisition is faster when A+ is more intense or greater in magnitude.	Expert suggestion		A	3	1	2	1	0	7
	Extinction										
4.1	Extinction	The CR decreases when CS–US pairings are followed by presentations of the CS alone or by unpaired CS and US presentations.	Alonso & Schmajuk	2.1/9.1	AA	12	0	2	0	0	14
4.2	Counterconditioning	CS–US training with an aversive US diminishes an appetitive CR otherwise produced by prior CS–US	Alonso & Schmajuk	9.3	AA	7	3	1	1	0	12

		training with an appetitive US (and conversely).									
4.3	ABA renewal	If CS-US acquisition takes place in context A and extinction in context B, then testing the CS in context A produces a stronger CR than in context B.	modified from Alonso & Schmajuk	2.3/10.7	AA	9	2	2	0	0	13
4.4	ABC renewal	If CS-US acquisition takes place in context A and extinction in context B, then testing in novel context C produces a stronger CR to the CS than in context B.	modified from Alonso & Schmajuk	2.3/10.7	B	5	1	3	5	0	14
	CS/US preexposure effects										
7.1	US pre-exposure effect	Presentation of the US in a training context prior to CS-US pairings retards the acquisition of the CR to the CS.	Alonso & Schmajuk	8.5/8.9	A	4	3	2	0	0	9

Table 3. Benchmarks graded A by the panel.

Number	Phenomenon	Description	Source		Survey grading						
					Median	AA	A	B	C	D	n
	Acquisition										
1.7	Timing of the CR	Peak of the CR tends to occur near the end of relatively long ISIs.	Alonso & Schmajuk	12.4, 12.9	A	8	5	3	1	0	17
1.8	Negatively accelerated learning curves	Group-averaged CRs tend towards an asymptote during acquisition.	Survey suggestion, modified from Alonso & Schmajuk	12.5	AA	13	3	2	1	0	19
1.9	Intertrial interval (ITI) and trial spacing effects	CRs are acquired faster and/or are stronger after acquisition when trials with the same CS are further apart in time during training.	Alonso & Schmajuk	12.2-3	AA	8	4	2	0	0	14
1.10	Scalar invariance in response timing	The variability of CR timing scales with mean CR timing.	Alonso & Schmajuk	12.6	A	3	3	1	1	2	10
1.11	Sensory preconditioning	When B-A pairings are followed by A-US pairings, presentation of B generates a CR.	Alonso & Schmajuk	11.1	A	6	6	7	0	0	19
1.12	Pavlovian-instrumental transfer	After Pavlovian acquisition, the presence of the CS influences instrumental behaviour to obtain/avoid the same US1 (outcome-specific PIT) or a different US2 (outcome-general PIT).	Survey suggestion		A	6	7	2	3	0	18
1.13	Summation	When two CSs independently trained with the same US are tested in combination, CRs are often greater than those exhibited to either CS individually.	Alonso & Schmajuk	6.1	A	5	6	4	1	0	16
	Generalisation										
2.3	Asymmetry in generalisation	Generalisation of inhibition is broader than generalisation of excitation.	Expert suggestion		A	2	2	1	3	0	8
2.4	Prototype and exemplar effects in category learning	After training with a set of related CSs, each independently presented with the same US, responding is stronger to trained exemplars than to untrained stimuli of the same category, and stronger to a novel	Expert suggestion		A	2	1	3	0	0	6

		stimulus that represents the average of the trained CS set (the prototype) than to exemplars.										
	Discrimination											
3.4	Negative patterning	After training with intermixed presentations of two individual stimuli followed by an outcome (A+, B+) and a compound of those two stimuli followed by no outcome (AB−), responding to the individual stimuli is stronger than responding to the compound.	Alonso & Schmajuk	4.3	A	3	6	1	0	0	10	
3.5	Positive patterning is easier than negative patterning	Given a discrimination in which the compound of two stimuli (AB) leads to a different consequence than the two stimuli individually (A / B), the learner acquires the discrimination faster when the compound predicts the outcome (positive patterning) than when the compound predicts the absence of the outcome (negative patterning).	Alonso & Schmajuk	4.4	A	4	5	0	1	0	10	
3.6	Biconditional discrimination	After training with intermixed presentations of stimulus compounds in which no single stimulus signals the presence or absence of the outcome but each compound predicts the presence or absence of the outcome (AB+ / BC− / CD+ / AD−), responding is higher for the compounds that predict the outcome.	Alonso & Schmajuk	4.7	AA	6	2	0	1	0	9	
3.7	Biconditional is harder than component discrimination	Discriminative responding between the outcome-present and outcome-absent trials of a biconditional discrimination (AB+ / BC− / CD+ / AD−) is slower than discriminative responding between the outcome-present and outcome-absent trials of a component discrimination that is matched for complexity but in which single stimuli signal the presence or absence of the outcome (AB+ / BC− / BC− / AD+).	Alonso & Schmajuk	4.9	AA	4	3	0	1	0	8	
3.8	Simultaneous feature-positive discrimination	Simultaneous presentations of two stimuli paired with a US (AX+), intermixed with presentations of one stimulus with no US (X−), result in stronger responding to the compound (AX) than to the single stimulus (X) alone, and strong responding in the presence of the other stimulus (A).	Alonso & Schmajuk	4.12	AA	7	2	0	2	0	11	
3.9	Serial feature-positive discrimination	Serial presentations of two stimuli paired with the US (A).	Alonso & Schmajuk	4.13/12.8	B	1	3	4	1	0	9	
3.10	Simultaneous feature-negative discrimination	Presentations of one stimulus paired with a US (X+) intermixed with simultaneous presentations of two stimuli without the US (AX−), result in stronger responding to the single stimulus (X) alone than to the compound (AX), while the other stimulus (A) acquires the ability to suppress responding when combined with another stimulus that has been paired with the outcome.	Alonso & Schmajuk	4.14	A	3	3	3	0	1	10	
3.11	Serial feature-negative discrimination	Presentations of one stimulus paired with a US (X+) intermixed with simultaneous presentations of two stimuli without the US (AX−), result in stronger responding to the	Alonso & Schmajuk	4.15	B	0	1	5	0	0	6	

		single stimulus (X) alone than to the compound (AX), while the other stimulus (A) acquires the ability to suppress responding when combined with another stimulus that has been paired with the outcome.										
3.12	Resistance of occasion setting to extinction and counterconditioning	After serial feature-positive or feature-negative discrimination, the ability of the feature to disambiguate the target is resistant to extinction and counterconditioning.	Expert suggestion		A	1	2	1	1	0	5	
	Extinction											
4.5	Protection from extinction	After pairing stimulus A with US, and conditioned inhibition training with stimulus B, presenting AB-noUS compounds leads to a higher CR to A alone, compared to conventional extinction (A-noUS presentations).	Survey suggestion		A	3	3	2	1	0	9	
4.6	Partial-reinforcement extinction effect	Extinction is slower following partial rather than continuous reinforcement.	Alonso & Schmajuk	2.2	AA	7	3	4	0	0	14	
4.7	Contingency degradation	Interspersing unsignalled US presentations during CS-US acquisition reduces the CR.	Survey suggestion		AA	6	2	3	0	0	11	
4.8	Spontaneous recovery	Presentation of the CS some time after successful extinction partially restores the CR.	Alonso & Schmajuk	10.6	A	6	5	4	0	0	15	
	Inhibitory conditioning											
5.1	Conditioned inhibition/Simultaneous feature-negative discrimination	After interspersed AB-noUS presentations and B-US pairings, A reduces the CR when paired with a US-predictive C (summation test), and when A is paired with the US, acquisition of a CR is retarded (retardation test).	Alonso & Schmajuk	5.1	AA	6	1	1	0	0	8	
5.2	Conditioned inhibition/Negative contingency training	After interspersed A-noUS and unsignalled US presentations, A reduces the CR when paired with a US-predictive B (summation test), and when A is paired with the US, acquisition of a CR is retarded (retardation test).	Alonso & Schmajuk	5.2	A	1	2	3	0	0	6	
	Stimulus competition/potentiation											
6.1	Overshadowing	Conditioning to the compound AB results in a weaker CR to B than is attained with B-US pairings.	Alonso & Schmajuk	7.5/7.6	AA	8	1	0	0	0	9	
6.2	Forward blocking	Conditioning to a compound AB results in weaker conditioning to B when the former is preceded by conditioning to A than when it is not.	Alonso & Schmajuk	7.2	AA	4	1	3	0	0	8	
6.3	Superconditioning	Reinforced AB presentations following inhibitory conditioning of A increase the CR to B as compared with when B is trained in the absence of A.	Alonso & Schmajuk	7.9	A	3	5	2	0	0	10	
	CS/US preexposure effects											
7.2	CS pre-exposure effect (latent inhibition)	Pre-exposure to a CS followed by CS-US pairings retards the acquisition of the CR.	Alonso & Schmajuk	8.1	AA	5	4	1	0	0	10	

7.3	A change of context disrupts latent inhibition	NA	Alonso & Schmajuk	8.2	A	2	3	1	1	0	7
7.4	Pre-exposure to a discriminant CS facilitates learning (perceptual learning)	Exposure to similar stimuli, CS1 and CS2, leads to faster subsequent acquisition of a discrimination between them.	Alonso & Schmajuk	8.7	AA	5	3	1	0	0	9

Table 4. Benchmarks graded B by the panel.

Number	Phenomenon	Description	Source		Survey grading						
					Median	AA	A	B	C	D	n
	Acquisition										
1.14	Conditioned diminution and facilitation of the unconditioned response	After acquisition, the response to the US in a CS-US presentation is diminished or facilitated compared to the US not preceded by CS, depending on the setup and species.	Alonso & Schmajuk	1.4	A	4	2	4	1	0	11
1.15	Imperfect predictors effect	An association CS-US2 is learned more rapidly after training CS-US1 with partial reinforcement rather than full reinforcement.	Alonso & Schmajuk	1.6	B	0	1	3	3	0	7
1.16	Learned predictiveness effect	After training with compound CS such that one component A always predicts US1 while another component B is sometimes coupled with US1 and sometimes with US2, the association A-US3 will be more rapidly learned than B-US3.	Expert suggestion		B	0	4	7	0	0	11
1.17	More intense CSs facilitate acquisition	When CSs are further away from a perceptual baseline (usually more intense), acquisition is faster or the CR asymptote is higher.	Survey suggestion		A	8	3	3	3	0	17
1.18	Backward conditioning elicits CRs	NA	Survey suggestion		B	0	3	5	8	0	16
1.19	Acquisition is context-dependent	A CR is stronger when tested in the same context as opposed to a different context from acquisition.	Survey suggestion		B	6	2	6	4	1	19
1.20	Cue-to-consequence effect	Some combinations of CS and US elicit stronger CR than others.	Survey suggestion		AA	10	3	2	2	0	17
1.21	Benefit of retrieval practice	Repeated retrievals increase the CR.	Survey suggestion		A	1	3	3	1	0	8
	Discrimination										
3.13	Interference by a common cue in negative patterning	When training with intermixed presentations of two individual stimuli followed by a US (A+, B+) and a compound of those two stimuli followed by no US (AB-), the discrimination is acquired slower when a common stimulus is added to all trials (AX+ / BX+ / ABX-).	Alonso & Schmajuk	4.5	A	0	4	4	0	0	8
3.14	Biconditional discriminations are harder than negative patterning	Discriminative responding between the US-present and US-absent trials of a biconditional discrimination (AB+ / BC- / CD+ / AD-) is more difficult than a discrimination between the US-present and US-absent trials of a	Alonso & Schmajuk	4.8	B	0	4	2	3	0	9

		negative patterning discrimination (A+ /B+/ AB-).									
3.15	Intra/extradimensional shift effects	After discrimination training with CSs that differ on two perceptual dimensions, one CS predicting the US and another not, a subsequent discrimination with different CSs is facilitated if the previously predictive dimension continues to be predictive and the other one not, rather than the other way around.	Expert suggestion		A	2	6	0	0	0	8
3.16	Transfer along a continuum (easy-to-hard effect)	Discrimination training with two CSs that are highly discriminable facilitates subsequent discrimination training with CSs that are more similar to each other.	Alonso & Schmajuk	9.4	A	0	6	3	0	0	9
	Extinction										
4.9	Reinstatement	After extinction, presentation of the US in the same context partially restores responding.	Alonso & Schmajuk	10.8	A	6	3	5	1	0	15
4.10	Rapid reacquisition	After CS-US acquisition and CS-noUS extinction, further CS-US presentations result in re-acquisition of the CR in fewer trials than during initial acquisition.	Alonso & Schmajuk	9.2	AA	6	4	1	1	0	12
4.11	Recovery from counterconditioning	After counterconditioning, the initial CR is partially recovered by the passage of time (spontaneous recovery), unsignalled US presentations (reinstatement), or change of context (renewal).	Expert suggestion		AA	3	1	2	0	0	6
4.12	Attenuation of renewal by multiple context extinction	Conducting extinction in multiple contexts, rather than a single context, reduces the CR when testing occurs in the original acquisition context or an entirely novel context.	Expert suggestion		B	0	3	6	3	0	12
4.13	Attenuation of renewal by retrieval cues	After interspersing a specific stimulus during extinction training, the presence of this stimulus reduces the CR when tested in the original acquisition context or a novel context.	Expert suggestion		A	1	1	1	1	0	4
4.14	AAB renewal	If both CS-US acquisition and extinction take place in context A, then testing in context B produces a higher CR to the CS than in context A.	modified from Alonso & Schmajuk	2.3/10.7	A	4	4	5	0	0	13
	Inhibitory conditioning										
5.3	Conditioned inhibition/Differential conditioning	After interspersed A-noUS presentations and B-US pairings, A reduces the CR when paired with a US-predictive C (summation test), and when A is paired with the US, acquisition of the CR is retarded (retardation test).	Alonso & Schmajuk	5.6	AA	3	1	0	2	0	6
5.4	Extinction resistance of conditioned inhibition	After interspersed A-noUS presentations and B-US pairings, A reduces the CR when paired with a US-predictive C (summation test), and when A is paired with the US, acquisition of the CR is retarded (retardation test).	Alonso & Schmajuk	5.3	A	3	1	0	3	0	7

	Stimulus competition/potentiation										
6.4	Relative validity	The CR to CS A is weaker when training consists of AB-US pairings alternated with AC-noUS trials than when it consists of AB trials alternated with AC trials, with each type reinforced half of the time.	Alonso & Schmajuk	7.1	A	5	3	2	0	1	11
6.5	Overexpectation	Reinforced AB presentations following independent reinforced presentations of A and B result in a decrement in the CR to A and B separately.	Alonso & Schmajuk	7.8	AA	6	3	1	1	0	11
6.6	Unblocking by increasing (or decreasing) the US	Increasing (or decreasing) the US during Phase 2 AB training increases responding to the blocked B.	Alonso & Schmajuk	7.3/7.4	A	3	5	1	0	1	10
6.7	Backward blocking	When AB-US pairings in Phase 1 are followed by A-US pairings in Phase 2, the CR to B is weaker than without the A-US pairings.	Alonso & Schmajuk	7.7	B	2	2	5	1	0	10
6.8	Unequal changes in responding by elements as a result of compound pairings (compound conditioning)	Unequal changes in CR to two CSs trained in compound occur when the CSs start with different response potentials.	Alonso & Schmajuk	7.10	A	3	4	2	0	0	9
6.9	Recovery from overshadowing	Extinction of the overshadowing cue results in increased responding to the overshadowed cue.	Alonso & Schmajuk	10.2	B	3	2	5	0	1	11
6.10	Overshadowing is stronger than external inhibition	Adding a CS to a trained compound of two CS results in a smaller decrease in CR than does removing a CS from the same compound.	Alonso & Schmajuk	3.3	A	0	4	0	0	0	4
6.11	Redundancy effect	Stronger responding to the blocked stimulus B after A-US/AB-US pairings than to an irrelevant stimulus B after AB-US/BC-noUS pairings.	Expert suggestion		B	1	1	4	2	0	8
	CS/US preexposure effects										
7.5	Context pre-exposure facilitates aversive CRs to the context	NA	Alonso & Schmajuk	8.4	B	0	3	3	1	1	8
7.6	Hall–Pearce effect	Training CS–weak US leads to slower acquisition of CS–strong US.	Alonso & Schmajuk	8.8	A	2	3	3	1	0	9
7.7	Learned irrelevance	Random interspersed presentations of the CS alone and the US alone retard conditioning even more than combined latent inhibition and US pre-exposure.	Alonso & Schmajuk	8.6	A	1	5	1	2	0	9

Table 5. Benchmarks graded C by the panel.

					Survey grading						
Number	Phenomenon	Description	Source		Median	AA	A	B	C	D	n
	Acquisition										
1.22	Partial reinforcement acquisition effect	Acquisition is slower or the CR asymptote is lower during partial	Alonso & Schmajuk	1.2	A	7	7	3	1	0	18

[illegible]

6.12	Recovery from forward blocking	Several different post-blocking manipulations result in increased responding to the blocked cue.	Alonso & Schmajuk	10.3	B	3	1	3	0	3	10
6.13	Recovery from backward blocking	Extinction of the blocker A results in increased responding to the blocked B.	Alonso & Schmajuk	10.4	A	2	2	3	1	0	8
	CS/US preexposure effects										
7.8	Following CS-pre-exposure and conditioning, a long relative to a short delay before testing decreases CRs (super latent inhibition)	NA	Alonso & Schmajuk	8.11/8.10	B	0	2	2	0	2	6
7.9	Presentation of a different CS before conditioning disrupts latent inhibition	NA	Alonso & Schmajuk	8.3	B	0	1	2	0	1	4
7.10	Recovery from latent inhibition (LI) induced by context extinction	LI is attenuated by extensive exposure to the training context between CS pre-exposure and the CS-US pairings or between the CS-US pairings and testing.	Alonso & Schmajuk	10.1	A	1	2	2	0	0	5

Results

Table 2-5 list all benchmarks ordered by topic, and within topics by their grading. Some benchmarks refer to a quantitative comparison between two other benchmarks; in such cases the comparison sometimes appears before the weaker of the two benchmarks is presented. We do not regard examination of this table as a substitute for reading the fuller descriptions of the phenomena and bases for the ratings. However, the table may serve as a helpful guide. In the main text, we discuss benchmarks graded as AA-A by either the authors or in the expert survey whereas the full description of the other benchmarks can be found in supplemental material. The grading is added in parentheses after the benchmarks name. For benchmarks that are not universal (i.e., not graded AA), we add the domain within which they have been demonstrated. As benchmarks differ in their generality, these domain descriptions are rather heterogeneous. For some benchmarks, particularly those with relatively diverse literature and without recent comprehensive reviews, a more detailed literature overview is found in Table S2.

1 Acquisition

In this section, we group benchmarks that constitute robust boundary conditions to the acquisition of a CR, or relate to the effects of presenting a CS after conditioning.

1.1 Acquisition (AA)

After a number of CS–US pairings, CS elicits a conditioned response (CR) that corresponds to a consistent increase or decrease in magnitude or frequency of an observable behavior.

After a CS and a US are experienced together at least once, but typically multiple times, a CR emerges upon presentation of the CS alone. When the US occurs independent of the agent's actions, this is referred to as classical or Pavlovian conditioning. A number of species-, domain-, and sometimes procedure-specific CRs and combinations of CRs have been observed, including overt motor behavior (e.g., freezing, and approach or withdrawal), autonomic nervous system responses (e.g., bradycardia, or sweating observed by skin conductance responses), and modulation of other behaviors (e.g., fear-potentiated startle or conditioned suppression of instrumental behavior).

Instrumental conditioning refers to the situation in which the US is contingent on a particular action determined by the environment, including an experimenter. In this case, this action is usually termed *instrumental* rather than *conditioned* response, and the US is commonly referred to as the outcome or reward. Famously reported by Pavlov (1927) and Thorndike (1898), for the classical and instrumental cases, respectively, these phenomena have been widely demonstrated for CSs across all sensory modalities (including discrete cues and configurations of objects often termed *contexts*), many types of aversive and appetitive USs, a very large number of experimental procedures, and across the animal kingdom, including invertebrates, insects, fish, birds, and a large

number of mammal species including humans. Although not part of this review, acquisition has occasionally been reported outside the animal kingdom (e.g., in unicellular organisms and plants, Carrasco-Pujante et al., 2021), although the evidence appears less consistent (Adelman, 2018; Markel, 2020).

Acquisition is subject to multiple boundary conditions. These boundary conditions are often very robust and replicable, and many (although not all) of the benchmarks in this list indeed constitute boundary conditions to acquisition as a result of CS-US pairings.

1.2 Benefit of spatiotemporal contiguity (AA)

CRs are stronger when CS and US are presented close in space and time.

CRs are often stronger if the US appears close in time and space to the CS (in Pavlovian conditioning) or instrumental action (in instrumental conditioning), respectively. This finding is highly robust across species, experimental procedures, and stimuli.

Among many examples, strong temporal contiguity has been shown to facilitate classical conditioning of salivary responses in dogs (Pavlov, 1927), eyeblink in rabbits (M. C. Smith, 1968a), and withdrawal responses in humans (Wolfe, 1932). The effect is readily observed in instrumental conditioning procedures as well, with humans (Shanks et al., 1989) and non-human animals (Dickinson et al., 1992; for a review, see Boakes & Costa, 2014) – see also the effect of inter stimulus interval, benchmark 1.3, below. Pavlovian conditioning is also weaker if an empty trace interval is inserted between the CS offset and the US onset (Pavlov, 1927). The literature demonstrating facilitation of CRs by strong cue-outcome spatial contiguity is more limited but still compelling, including for instance simple conditioning with doves (Christie, 1996), second-order conditioning in auto-shaping with pigeons (Rescorla & Cunningham, 1979), and sensory preconditioning in humans (Renaux et al., 2017).

Despite being robust, the impact of contiguity on conditioned responding is modulated by multiple factors. Although conditioning degrades monotonically with increasing temporal delays between CS and US, the decay slope can be notoriously variable from one procedure to another (see also benchmark 1.3: ISI effects). Whereas some procedures, such as eyelid conditioning (Kimble, 1947), require delays shorter than one second, other procedures, most famously conditioned taste aversion, can tolerate delays in the range of hours (Garcia et al., 1966). Conversely, close contiguity, on its own, does not suffice to produce reliable conditioned responding as can be seen in overshadowing (see benchmark 6.1). In the case of studies with humans, the extent to which delays affect CR seems to be modulated by participants' expectations (Buehner & May, 2003).

1.3 Interstimulus interval (ISI) effects (AA)

Strongest CR with relatively short ISIs.

See Table S2.

Changes to the interstimulus interval (ISI), that is, the time between the onset of the CS and the onset of the US, affect how quickly and strongly a CR is acquired (e.g., M. C. Smith, 1968b). Typically, this relationship between the length of the ISI and CR follows an inverted-U shaped function: CRs are acquired most quickly and strongly with intermediate ISIs, while very short or longer ISIs results in slower or weaker acquisition, or no acquisition at all (for a review, see Nasser & Delamater, 2016). Notably, this phenomenon is observed when the CS and US overlap, that is, maintaining strong temporal contiguity between them.

The inverted U-shaped function has been observed across various procedures and species, including conditioned suppression in rats (Yeo, 1974), fear conditioning in cats (autonomic responses and paw withdrawal; Wickens et al., 1969), rhesus monkeys (Noble

& Harding, 1963), and humans (Prokasy et al., 1962), eyeblink conditioning in rabbits (Frey & Ross, 1968) and humans (Hartman & Grant, 1962), odor avoidance-approach conditioning in fruit flies (Tanimoto et al., 2004), and salivary conditioning in dogs (Ost et al., 1968). ISI ranges differ by species and procedures, from milliseconds in rabbit eyeblink conditioning to seconds in conditioned suppression in rats (see Table S2 for details).

While many studies align with the inverted U-shaped function, Holland (1980) suggested that the function's shape may depend on the CR being measured. Additionally, research indicates that the strength of the CR is better predicted by the ratio of the intertrial interval (ITI) to the ISI, rather than by either factor alone (see Gibbon & Balsam, 1981). Finally, evidence suggests that the reduced overall CR with long ISIs often results from the development of inhibition of delay, where response latencies increase with the ISI length, creating the false impression of weaker acquisition (Vogel et al., 2003a).

1.4 Second-order conditioning (AA)

When A-US pairings are followed by B-A pairings, presentation of B generates a CR.

Pavlov (1927) contrasted *first-order conditioning*, in which a to-be-tested CS is paired directly with the US, to *second-order conditioning*, in which the to-be-tested CS is never directly paired with the US. Concisely, the design summary would be: A->US; B->A or B+A; test B and observe greater CR to B compared to appropriate controls.

Although Pavlov (1927) initially reported that responding in second-order conditioning was relatively weak, it has subsequently proved to be a highly reliable effect observed in a wide variety of species and preparations (Amiro & Bitterman, 1980; Brembs & Heisenberg, 2001a; M. Cook & Mineka, 1987; Craddock et al., 2018; Gibbs et al., 1991; Lee & Livesey, 2012; Rashotte et al., 1977; Rescorla & Cunningham, 1979; Rizley & Rescorla, 1972). However, the number of BA pairings is one very general boundary

condition on excitatory second-order conditioning. With increasing number of BA pairings the degree of CR to B decreases, and with extensive BA pairings, B can become a conditioned inhibitor of the US (e.g., Herendeen & Anderson, 1968; Holland & Rescorla, 1975; Yin et al., 1994). The parameter dependence of second-order conditioning and its absence after extended training can be modulated by other design parameters, for example simultaneous B+A as opposed to serial B->A pairings favor the development of conditioned inhibition (Stout et al., 2004).

Furthermore, procedural variations have an impact and there are a number of cases where manipulations have dissociable effects on second-order conditioning as opposed to direct/first order conditioning. Interestingly, many of these dissociations overlap with those seen between sensory preconditioning (see benchmark 1.11) and direct conditioning. For example, introducing a delay between A and the presentation of the US, which typically results in less excitatory responding to A being observed than without such a delay has little effect on responding to B and may actually increase it (Barnet & Miller, 1996; Lin & Honey, 2011); while reversing the first-order conditioning stage (i.e., US before A) does not eliminate responding to B, but does typically reduce/remove responding to A (Barnet et al., 1997) – see also benchmark 1.18 (backward conditioning). Moreover, there have been repeated reports of maintained responding to B after the response to A was extinguished (e.g., Amiro & Bitterman, 1980; Archer & Sjöden, 1982; Craddock et al., 2018; Rizley & Rescorla, 1972) although responding to B does appear to be more sensitive to extinction of A when the B+A pairings were simultaneous (Rescorla, 1982). In addition, there can be qualitative differences in CR pattern between the directly conditioned A and the second-order conditioned B (Stanhope, K. J., 1992). As with sensory preconditioning (see benchmark 1.11), dissociations of this sort between the CRs to B and A have been mainly considered as

indicators of the nature of the learning process(s) underpinning second-order conditioning, which is beyond the scope of the current article (Gostolupce et al., 2022; Honey & Dwyer, 2022).

As a direct instrumental analogue of classical second-order conditioning, response-contingent delivery of A can support the acquisition of instrumental responding, provided A has previously been paired with a US (e.g., Mackintosh, 1974, chapter 5; Parkinson et al., 2005).

1.5 Recency effect (AA)

After acquisition, CRs are stronger when the test is closer in time to acquisition.

The training-test recency effect is, along with acquisition, one of the two most ubiquitous phenomena in associative learning. The effect was first systematically studied in non-associative learning by Ebbinghaus (1885), who found gradual forgetting of nonsense syllables over periods up to several weeks. It has later been widely observed across many species on many different associative learning tasks including Pavlovian and instrumental conditioning, in the natural habitat as well as in the laboratory.

The performance decrement seen over increasing retention intervals is negatively decelerating, with research suggesting either an approximately exponential or power function (see White, 2001), although there is still considerable uncertainty about the exact shape of this function (Parra & Radvansky, 2024).

As all tasks are, in one way or another, retroactive interference tasks in the sense that retention intervals are invariably filled with new events, the benefit of recency of target training to test performance is opposed by the detrimental effects of recency of potentially interfering training (Kraemer & Golding, 1997). Accordingly, there is evidence that recency is a minor factor (and forgetting is not observed) in some procedures in

which interference is minimal such as taste aversion learning (Revusky & Garcia, 1970; Steinert et al., 1980).

While the recency effect is very general, it must be borne in mind that degraded performance over increased retention intervals can often be restored by diverse treatments (e.g., reinstatement, better retrieval cues at test, fewer interference cues at test; see Miller, 2021). Indeed, there are even some effects, such as incubation of conditioned fear (Pickens et al., 2013), in which CRs increase with longer retention intervals.

1.6 Post-training US revaluation (AA)

After CS-US pairings, revaluation of the US (e.g., by feeding to satiety) affects the response to the CS.

US devaluation (e.g., by pre-test feeding of a food US to satiation or pairing a rewarding US with an aversive outcome such as lithium chloride induced nausea) results in a decrease in CR, and US inflation can increase the response to the CS (albeit studies of US devaluation are much more numerous). This effect is seen even without additional experience with CS and US pairings. The effect has been reported in a very wide range of species, including humans (Hosoba et al., 2001), rats (Holland & Straub, 1979) quail (Hilliard & Domjan, 1995), snails (Muñiz Moreno & Loy, 2023) newts (Taniuchi, 2016), trout (Nordgreen et al., 2010), crickets (Mizunami et al., 2019) and honeybees (Lai et al., 2020), and within well-studied species (in particular rats) in multiple preparations and developmental stages (Dwyer, 2005; Kraemer et al., 1992; Morrison et al., 2015) including instrumental procedures (Adams, 1982). Although direct comparisons are limited, the effects of devaluing the US may be larger and more reliable than the effects of increasing the value of the US, and changing the value of aversive USs may be more difficult than

changing the value of appetitive USs (compare De Jong et al., 1996; with Hosoba et al., 2001).

Despite the widespread observation of the effect, there are reports of differences in its size or presence as a function of the CR being assessed. For example in a human fear conditioning study, conditioned skin conductance was sensitive to US deflation and inflation, but ratings of CS valence were not (Hosoba et al., 2001). Additionally, examination of sign- and goal-tracking responses in rats has suggested that the former can be insensitive to US devaluation when the latter are not (Bien & Smith, 2023; Morrison et al., 2015; Nasser et al., 2015), although this is not a universal observation (Amaya et al., 2020; Derman et al., 2018). It is also worth noting that the sensitivity of instrumental conditioning to outcome devaluation can be reduced or removed with extended training (Adams, 1982), whereas the sensitivity of Pavlovian responses to US devaluation appears to be maintained even with extended training (González et al., 2024; Holland, 1998a).

1.7 Timing of the CR (A)

Peak of the CR tends to occur near the end of relatively long ISIs.

Domains: Widely observed but not universal, and boundary conditions unclear.

See Table S2.

When combining a long ISI with extended training in classical conditioning, a reduction in the magnitude of the CR during the early part of the CS is typically observed. This results in the CR peaking closer to the expected time of the US, a phenomenon Pavlov (1927) referred to as “inhibition of delay”. Vogel et al. (2003b), using eyelid conditioning in rabbits, found that the latency to respond during the CS increased with training when relatively long ISIs were used (500, 1,000, and 2,000 ms). In contrast, for animals trained with a shorter ISI (250 ms), the latency to respond decreased rather than increased.

The increase in the latency of the CR peak over training has been observed across various procedures and species when manipulating ISI length, including salivary conditioning in dogs (Ost et al., 1968), pupillary dilation in cats (Oleson et al., 1973), autoshaping in pigeons (Osborne & Killeen, 1977), fear conditioning in goldfish (Drew et al., 2005), conditioned suppression in rats (Rosas & Alonso, 1996a), magazine conditioning in mice (Austen & Sanderson, 2019), eyeblink conditioning in rabbits (Kehoe et al., 2010a), and conditioned avoidance in dogs (Zieliński et al., 1979), rats (Zieliński et al., 1995), and humans (Molet et al., 2007). The range of ISIs spanned from 125 ms in eyeblink conditioning (Kehoe et al., 2010a) to 200 s in conditioned suppression in rats (Rosas & Alonso, 1996b). In most studies that were reviewed, the peak of responding shifted toward the end of the ISI over training, regardless of ISI length. Rosas and Alonso (1996b) found that the progressive increase in the latency of the CR peak was somewhat slower with their shortest ISI (50 s).

Temporal specificity of the CR peak commonly increases with a relatively short-duration cue, while longer ISIs tend to produce a broader and more variable CR (Kehoe et al., 2010b) (see benchmark 1.10, Scalar invariance in response timing). Less variable CR peak times with short ISIs have been reported in human salivary and heart rate conditioning, mouse magazine conditioning, and pigeon autoshaping. Additionally, a decrease in response latency, rather than an increase, with decreasing ISI has been reported in several eyeblink conditioning studies in rabbits, including a study that found a decrease in response latency with ISIs ranging from 250 to 4,000 ms (Schneiderman & Gormezano, 1964)—opposite to the increase in CR peak latency observed in other cases. Similarly, fear-conditioned pupil dilation in humans has been reported to occur with a constant latency after the CS, independent of ISI (Korn et al., 2017). Furthermore, US approach (often termed *goal-tracking*) appears to increase toward the end of the CS, while

CS approach (often termed *sign-tracking*) either decreases or remains relatively stable throughout the CS duration (e.g., Iliescu et al., 2020). Thus, the response system appears to be one of the factors influencing the pattern of the CR.

In summary, the CR peak tends to occur towards the end of the ISI for many response systems, but the relationship between ISI length and the timing of peak responding is not monotonic and may depend on a combination of factors, including training duration, the response system, and the conditioning preparation used in the study.

1.8 Negatively accelerated learning curves (A)

Group-averaged CRs tend towards an asymptote during acquisition.

Domains: Widely observed, but deviations occur, with unclear boundary conditions

The strength of the CR increases progressively with each new pairing of the CS and the US. Similarly, if the CS is presented on its own repeatedly after acquisition (extinction), the strength of CR decreases gradually. This increase/decrease is typically larger for initial than for late trials, resulting in a negatively accelerated curve.

Gradual and negatively accelerated acquisition and extinction curves are reported frequently in both classical and instrumental conditioning studies. For example, considering only articles published in the *Journal of Experimental Psychology: Animal Learning and Cognition* during 2023, gradual acquisition or extinction curves were reported in procedures as diverse as discrimination learning in pigeons (R. G. Cook, Brooks, et al., 2023; R. G. Cook, Qadri, et al., 2023) and rats (Bond et al., 2023), conditioned taste aversion in rats (Marshall et al., 2023), human causal/predictive learning (Alcalá, Prados, et al., 2023; Lovibond et al., 2023), human instrumental learning (Reed, 2023; Thrailkill, 2023), and instrumental learning in rats (Fujimaki & Kosaki, 2023).

Following Hull (1943), some of the most popular formal models of conditioning predict that learning curves should follow an exponential function. However, learning curves of different (typically monotonic) shapes have been observed (Mazur & Hastie, 1978), including acquisition curves that are not uniformly negatively accelerated, such as sigmoid functions (e.g., Bathellier et al., 2013). Furthermore, it has been claimed that the negatively accelerated learning curves often reported in the literature could be a statistical artifact of group averaging, potentially hiding radically different acquisition functions at the individual subject level (Estes, 1956). Consistent with this, the analysis of individual learning curves sometimes shows evidence of sudden, step-wise changes in conditioned responding, either during acquisition (Gallistel et al., 2004) or extinction (Blanco & Moris, 2018). However, other studies have found evidence of negatively accelerated learning curves (e.g., J. A. Harris, 2011, 2022) or gradual curves with other monotonic shapes (Kehoe et al., 2008) at the individual level as well.

1.9 Intertrial interval and trial spacing effects (A)

CRs are acquired faster and/or are stronger after acquisition when trials with the same CS are further apart in time during training.

Domains: Widely observed across species, but not universal and with unclear boundary conditions

See Table S2.

When the inter-trial interval (ITI) is longer, all else being equal, learning progresses generally faster and to a higher asymptote. This has also been termed the *trial-spacing effect*, and procedures with short ITIs and long ITIs are sometimes referred to as *massed trials* and *spaced trials*, respectively. The effect is also found when trials with different CSs are intermixed at a constant ITI, and those trials in this sequence that have

the same CS are either massed or spaced. We are not aware of studies independently varying ITI and the effects of trial sequence.

Probably the first demonstration of a long ITI advantage was in human eyeblink conditioning (Spence & Norris, 1950), and this has been observed in various further domains including aversive (Barela, 1999) and appetitive (Holland, 2000) Pavlovian conditioning, conditioned taste aversion (Domjan, 1980), autoshaping (Terrace et al., 1975), and in species including fruit flies, sea slugs, pigeons, rats, rabbits, and, more rarely humans (see Table S2 for a detailed overview). There are also demonstrations in instrumental conditioning preparations (Gallistel & Shahan, 2024; Kalmbach et al., 2019). Several boundary conditions have been suggested but not consistently confirmed. Some studies, including a meta-analysis of pigeon autoshaping and a study on rats, suggest that conditioning strength is strongly determined by the ratio of ITI and CS time (Gallistel & Gibbon, 2000; Holland, 2000).

1.10 Scalar invariance in response timing (A)

The variability of CR timing scales with mean CR timing.

Domains: eyeblink conditioning with rabbits and ring doves; reward conditioning, with rats and pigeons; conditioned suppression and instrumental (Sidman) avoidance conditioning with rats; aversive conditioning in gold fish

See Table S2.

Scalar timing theory (Gibbon, 1977; Gibbon et al., 1984) posits that the perception of time possesses two key statistical features. The first is *mean accuracy*, that is, that the average time estimate for a given real duration, t , should match t . The second characteristic is the *scalar* property, which requires that the standard deviations of these time estimates increase proportionally with the mean. To assess the scalar property,

researchers often calculate the coefficient of variation (CV; standard deviation/mean), expecting it to remain constant across varying time intervals.

In conditioning procedures, this involves a training stage with CSs of varying duration. The CV is computed for peak CR timing across trials, which is taken as the measure of the animal's estimate of the time of US occurrence (see benchmark 1.9: timing of the CR).

An alternative way to verify scalar timing is to test whether the data conform to Weber's law, by examining whether the CRs (which reflect timing estimates) overlap when plotted on the same relative scale (the term *superimposition* is used in the supporting table).

In a conditioning context, both mean accuracy and scalar property of responses have been found in several Pavlovian conditioning studies (e.g., Brown et al., 1997; Leonard & Theios, 1967; Rosas & Alonso, 1996a) comprising multiple species, interval durations (ranging from tens to hundreds of seconds; see Table S2 for details), and learning domains (appetitive, aversive). This has also been reported in an instrumental Sidman avoidance task (Libby & Church, 1974). In humans, most evidence for temporal discrimination comes from temporal accuracy and discrimination tests (e.g., instrumental, implicitly reinforced conditioning). While demonstrated in several domains, there is only a limited number of investigations.

Boundary conditions have been suggested – notably that the phenomenon breaks down with very short and long CS-US intervals (Church et al., 1976; Fetterman & Killeen, 1992) – but are not systematically investigated.

1.11 Sensory preconditioning (A)

When B–A pairings are followed by A–US pairings, presentation of B generates a CR.

Domains: Domain- and species-general in Pavlovian conditioning but with circumscribed exceptions.

The term sensory preconditioning was coined by Brogden (1939) and is used here for any protocol with the steps outlined above. Note that some authors have proposed additional terminology to reflect sub-categories of this general design. Most important is *backwards sensory preconditioning* (Ward-Robinson & Hall, 1996), which is used to refer to designs where A preceded B during the initial pairing phase, and *mediated conditioning* (Holland, 1981) which is used to refer to situations in which the response to B is presumed to depend on excitatory B-US associations as opposed (for example) to a chain B-A-US. For the present purposes, there is no need to use such sub-categories, as they reflect theoretical assumptions about the underlying learning mechanism, which are beyond the scope of the current article.

The sensory preconditioning effect has been reported in a large number of species including *Drosophila* (Brembs & Heisenberg, 2001b), honeybees (Müller et al., 2000), pigeons (Reid, 1952), mice (Busquets-Garcia et al., 2017), rats (Lin & Honey, 2011a; Pfautz et al., 1978; Ward-Robinson & Hall, 1998a), rabbits (Pfautz et al., 1978), monkeys (Beauchamp & Gluck, 1988), and humans (Renaux et al., 2017). These observations were made in a variety of preparations including both appetitive and aversive reinforcement.

While the basic sensory preconditioning phenomenon is robust and general, procedural variations do have an impact on the effect and it is not always observed across all response measures. Moreover, there are a number of cases where manipulations have dissociable effects on sensory preconditioning as opposed to direct/first-order conditioning. Interestingly, many of these dissociations overlap with those seen between second-order conditioning and direct conditioning. For example, introducing a delay between A and the presentation of the US, which typically results in less excitatory

responding to A, has little effect on responding to B and may actually increase it (Cole et al., 1995; Lin & Honey, 2011b; Ward-Robinson & Hall, 1998b), while reversing the first-order conditioning stage (i.e., US before A) does not eliminate responding to B, but does typically reduce/remove responding to A (Barnet et al., 1997). Indeed, there are multiple reports of responding to B in the absence of observed responses to A (Dwyer, 2001; Holland, 1981, 1990). This includes at least one report where responding to B was seen after the response to A was extinguished (Ward-Robinson & Hall, 1996), although in other cases such extinction of responding to A did reduce responding to B (Rizley & Rescorla, 1972). In addition, in a sensory preconditioning procedure using flavors and taste aversion, the directly conditioned A elicited reduced hedonic reactions as well as a reduction in consumption, but the indirectly conditioned B only elicited reduced consumption (Dwyer et al., 2012). Dissociations of this sort between the response to B and A and/or the manipulations that produce them have been mainly considered in the literature as potential indicators of the nature of the learning mechanisms underpinning sensory preconditioning (and the possibility that different mechanisms might be engaged under different circumstances). Recent reviews (Gostolupce et al., 2022; Honey & Dwyer, 2022) have attempted some synthesis of such procedural variations, their effects, and the implications for the nature of learning produced by sensory preconditioning.

1.12 Pavlovian-instrumental transfer (PIT; A)

After Pavlovian acquisition, the presence of the CS influences instrumental behavior to obtain/avoid the same US1 (outcome-specific PIT) or a different US2 (outcome-general PIT).

Domains: Appetitive and aversive Pavlovian conditioning

See Table S2.

After Pavlovian conditioning with a CS-US1 coupling, and separate instrumental conditioning, instrumental CRs are modified in the presence of the Pavlovian CS. When US1 is appetitive, then instrumental responses to obtain the same US1 are increased compared to a different US2 (selective PIT), and instrumental responses to obtain a different US2 are increased compared to a no-CS instrumental baseline (general or non-selective PIT) (Badioli et al., 2024; Cartoni et al., 2016; Holmes et al., 2010). When US1 is aversive, instrumental responses to avoid the same US1 are increased (Rescorla, 1967), sometimes termed *conditioned facilitation*. A related effect is *conditioned suppression*, whereby instrumental responses to obtain an appetitive US2 are decreased in the presence of a CS that predicts an aversive US1. All these effects describe the impact of a Pavlovian CS beyond the CR observed during acquisition, and might be informative about the underlying learning mechanism.

In the appetitive domain, selective and non-selective PIT have been reported in at least 30 publications by different laboratories, with different procedures in mice, rats, rabbits, pigeons, monkeys, horses, and humans (for reviews, see Badioli et al., 2024; Cartoni et al., 2016; Holmes et al., 2010). However, there is considerable variability in effect sizes, some negative reports, and many moderators have been suggested in individual studies (Badioli et al., 2024; Cartoni et al., 2016), some of which were confirmed across experiments. In particular, a meta-analysis of 30 publications showed that when Pavlovian and instrumental training phases are separated, increased phase 1 training diminishes, and increased phase 2 training increases, selective and general PIT, regardless of whether phase 1 and 2 correspond to Pavlovian and instrumental training, respectively, or vice versa (Holmes et al., 2010).

In the aversive domain, PIT has been demonstrated by several laboratories (e.g., Rescorla, 1967; Weisman & Litner, 1969; Xia et al., 2019), including different species (rats,

dogs, and humans) and somewhat diverging procedures, but mostly based on Sidman avoidance (see Table S2 for details and Badioli et al., 2024 for a meta-analysis of human studies).

1.13 Summation (A)

When two CSs independently trained with the same US are tested in combination, CRs are often greater than those exhibited to either CS individually.

Domains: Pavlovian conditioning

Although sometimes used in a non-specific manner, the term summation here refers to the effect where, after two stimuli are separately trained with the same US (e.g., A+, B+), the CR to the compound of those stimuli is greater than to either of them tested alone. An early review of this phenomenon (Weiss, 1972) noted second-hand reports dating back to Pavlov's laboratory, as well as many contemporaneous reports in different species and preparations (including instrumental procedures as well as Pavlovian ones). A more recent and systematic review of summation in Pavlovian procedures (Ghirlanda, 2022) notes that summation is reported reliably for rabbits (nictitating membrane response), pigeons (autoshaped keypress), rats (autoshaped magazine approach and conditioned suppression), and humans (electrodermal responses and causal learning). While summation is typically defined (and investigated) in terms of the response to a compound of two stimuli previously trained separately with the same outcome compared to the response elicited by each stimulus tested alone, it should be noted that this compound/element comparison is confounded in several ways, in particular in regard to the complexity of the stimuli and overall sensory intensity (assuming two stimuli combined will be more intense than either one alone). Although used on fewer occasions than the typical summation design, there are reports across several species that after reinforced training with A and B separately, responding is higher to the AB compound

than to a similar compound (e.g., CD) that had been reinforced as a compound (Aydin & Pearce, 1997; Rescorla, 1997b; Soto et al., 2009).

While the basic phenomenon of summation is reliable and general, procedural variations do have an impact on the results and it is not always observed. The most well-studied moderator of the summation effect is whether the two stimuli A and B come from the same or different modalities (e.g., one visual and one auditory compared to two visual or two auditory stimuli). Direct comparisons between summation effects using stimuli from the same versus different modalities suggest that the effect is larger when stimuli from different modalities are used, for example, in pigeons (Aydin & Pearce, 1997), rabbits (Kehoe, 1986), humans (Redhead, 2007), and rats (Thein et al., 2008). The idea that summation effects are considerably larger with stimuli from different modalities than when they are drawn from the same modality is also supported by meta-analytic methods (Ghirlanda, 2022) although it should be noted that there are relatively few studies with rats or humans compared to rabbits or pigeons.

In addition, a comprehensive review (Ghirlanda, 2022) suggested that not only are summation effects generally smaller for within-modality experiments than between-modality ones, but summation may not be reliably observed at all for the within-modality experiments (albeit, this is based on relatively few studies in a few preparations – with the bulk of studies of summation using between-modality designs). It has also been suggested that, in human causal learning, the summation effect is larger if participants assume the two stimuli are independent predictors of the outcome than otherwise (Pérez et al., 2018). Ghirlanda's review supports this suggestion (Ghirlanda, 2022).

2 Generalization

In this section, we group benchmarks that relate to CR elicited by stimuli that are similar to a trained CS.

2.1 Generalization (AA)

A novel cue elicits a CR to the degree that it shares some characteristics with a CS that has been paired with the US.

Stimulus generalization is the phenomenon where responses conditioned to one CS transfer to a novel generalization stimulus (GS) as a direct function of the GSs similarity to the trained CS. As cues are never replicated exactly, learning would be inconsequential without generalization. Generalization was first reported by Pavlov (1927) in his experiments on conditioned salivation in dogs. In a typical experiment, a Pavlovian or instrumental response is first acquired to a CS. A generalization gradient is then obtained by plotting responses to GSs varying on a dimension of the CS. Guttman and Kalish (1956) were the first to report generalization gradients in an instrumental conditioning procedure. Critically, they maintained a high level of responding during testing by presenting intermittent USs. Although generalization is often assessed over a continuous CS dimension (e.g., wavelength, size), any stimuli can be presented in the generalization test (discrete or compound).

Generalization is extremely robust, and regarded as a fundamental phenomenon with universal characteristics (Ghirlanda & Enquist, 1998; Rescorla, 2006; Shepard, 1987). The shape of the gradient typically follows a decreasing function as stimuli become more dissimilar to the trained stimulus (Shepard, 1987), with a few exceptions (e.g., Razran, 1949; Wills & Mackintosh, 1998). Generalization has been observed in numerous species (e.g., humans, rats, pigeons, and chickens), preparations (e.g., fear conditioning, pigeon autoshaping, human predictive learning, instrumental conditioning), stimulus dimensions, and various CRs. Generalization is such a reliable phenomenon that research in this area usually aims to identify factors that determine the form of generalization

(Honig & Urcuioli, 1981; Mackintosh, 1974) or the degree of generalization decrement (i.e., the degree to which generalization fails or is incomplete).

A small number of studies report a lack of generalization, but these have employed GSs that were relatively dissimilar to the CS (e.g., tones differing in 1 or 2 octaves, Wickens, 1943). These cases, due to the shape of generalization gradients, appear to be a feature of generalization, rather than a boundary condition.

2.2 Peak and area shift (AA for area shift; A for peak shift)

After intradimensional discrimination training, generalization gradients increase beyond the CS+, in the opposite direction from the CS-.

Peak shift and area shift are generalization phenomena that are established using intradimensional discrimination training: an animal learns to respond differentially to a CS+ and CS- located on the stimulus dimension that will be varied at test. Peak shift is observed if the peak of the post-discrimination generalization gradient shifts from the CS+ to a generalized stimulus in the opposite direction from the CS-. Area shift is observed if more than 50% of the area of a gradient lies on the side of the CS+ opposite to the CS- (Rilling, 1977). A stricter definition for area shift is when the area on the non-CS- side of the CS+ is greater than the gradient for a control group trained on CS+ only (Lovibond et al., 2020). Peak shift was first demonstrated by Hanson (1957, 1959) using instrumental conditioning, and can also be found in Pavlovian conditioning, as well as human two-choice discrimination learning such as predictive and category learning tasks. “Negative” peak shift can also occur, where the gradient is lowest not at the CS- but at a stimulus located in the opposite direction to the CS+. Negative peak shift is considered to be part of the same phenomenon (Guttman, 1965).

It is difficult to quantify the number of studies that have demonstrated peak shift. Some studies have used unusual analysis methods (Lee et al., 2021), or do not provide

statistical analyses at all. Ignoring these measurement issues, there are at least 100 published studies of peak shift involving humans and non-human species (e.g., pigeons, rats, horses, bees), preparations (instrumental and Pavlovian conditioning, two-choice discrimination tasks, stimulus identification tasks), stimulus dimensions (e.g., wavelength, line orientation, frequency, and faces), USs (appetitive and aversive), and readouts (e.g., different CR, outcome expectancy ratings, classification accuracy, and identification accuracy). Peak shift is thus domain- and species-general. Area shift is more robust than peak shift (Rilling, 1977) since a peak shift usually involves an area shift.

Although peak shift is considered a robust phenomenon, it is known to be parameter-dependent (Purtle, 1973), and variable between individuals (Lee et al., 2018; Rilling, 1977). Peak and area shifts require successful acquisition of the initial discrimination and attention to the to-be-varied dimension. Work by Terrace (1963), however, suggests that errors in performance are critical to observe peak shift (but see Rilling, 1977, for a critique). The degree of shift along the dimension has been found to be inversely proportional to the difference between the CS+ and CS- (Derenne, 2006; Hanson, 1959), but the opposite relationship has been found in humans (e.g., Doll & Thomas, 1967). Peak shift is more likely to be found with long training (Rilling, 1977), and early in generalization testing (e.g., Livesey & McLaren, 2009; Pierrel & Sherman, 1962). In humans, studies failing to show peak shift often produce sigmoidal, monotonically increasing gradients instead (e.g., Lee & Livesey, 2018; Wills & Mackintosh, 1998). There are some failures to replicate that do not have a clear explanation (see Purtle, 1973).

2.3 Asymmetry in generalization (A)

Generalization of inhibition is broader than generalization of excitation.

Domains: Mainly appetitive instrumental conditioning

Generalization gradients around a CS- are broader and shallower than the inverse of gradients around a CS+. This effect has been most clearly demonstrated using the interdimensional discrimination procedure in instrumental conditioning. In this procedure, one stimulus feature (e.g., line orientation, tone) is present in the CS+ and absent in the CS-, while another feature is present in the CS-, and absent in the CS+. Generalization is tested by varying the stimulus dimension and comparing gradients between groups. Note that generalization of inhibition specifically refers to generalization from a CS- that is correlated with the absence or reduction of the US. This definition excludes generalization of extinction (in which the same CS was previously reinforced), as well as generalization around a CS- that signals an outcome of a different valence to the CS+ (e.g., CS+ signals an appetitive US and CS- signals an aversive US).

The majority of published studies have used instrumental conditioning with pigeons. Honig and Urcuioli (1981) reviewed this literature and found that on balance, negative gradients are flatter than positive gradients. This finding has been demonstrated in pigeons (e.g., Jenkins & Harrison, 1962; Boneau & Honig, 1964; Hearst, 1968) and rats (Schwartzbaum & Kellicutt, 1962) using the interdimensional discrimination procedure. Rescorla (2006) also demonstrated the effect with a different procedure that avoids the issue of comparing gradients at different points on the response scale. He found more responding to a compound consisting of a trained excitator and inhibitor than a compound consisting of novel cues of the same color but different shape. This finding suggests that generalization from an inhibitor is broader than an excitator.

There are a few studies that did not observe asymmetrical inhibitory and excitatory gradients. Honig (1963) showed that when plotting gradients relative to total responses (not absolute responses), gradients of inhibition and excitation were symmetrical. Thomas and Lanier (1962) showed symmetrical generalization gradients in

humans, but the procedure was an instructed absolute identification task. One issue in investigating this phenomenon is that gradients of excitation and inhibition can change in different ways over repeated tests (Boneau & Honig, 1964).

2.4 Prototype and exemplar effects in category learning (A)

After training with a set of related CSs, each independently presented with the same US, responding is stronger to trained exemplars than to untrained stimuli of the same category, and stronger to a novel stimulus that represents the average of the trained CS set (the prototype) than to exemplars.

Domains: Mainly appetitive instrumental conditioning

A prototype can be regarded as a complex stimulus that is employed to generate specific training items, often by the addition of noise or extraneous features. For instance, in the classic task developed by Posner and Keele (1968), a specific array of random dots is jittered to generate training exemplars. The *prototype effect* refers to the finding that at transfer, responding is stronger to the previously-unseen prototype than to new exemplars.

This effect has been found in many species including humans (Posner & Keele, 1968), pigeons (e.g., Jitsumori et al., 2011), and monkeys (J. D. Smith et al., 2008), and with many types of stimuli and tasks including discrimination learning with both simple stimuli composed of independent features (Aydin & Pearce, 1994) as well as complex polymorphous materials (Jitsumori et al., 2011).

Alongside prototype effects, there is also evidence that responding is typically stronger at test to training exemplars than to new exemplars (Posner & Keele, 1968) – the exemplar or instance effect. Moreover, test items similar to both the prototype of one category and the training exemplars from a different category tend to be assigned on the basis of exemplar, not prototype, similarity (Dopkins & Gleason, 1997). Thus, compared

to new distortions created using the same generation method, both the prototype and the trained exemplars show enhanced responding at test.

3 Discrimination

In this section, we discuss benchmarks about learning to discriminate the antecedents of reinforcement and non-reinforcement, involving at least two different CS.

3.1 Differential/discriminative training (AA)

After receiving training in which one CS is followed by a US (CS+) and another CS is not followed by a US (CS-), the difference in responding to the two stimuli is greater than if only CS+ were trained and CS- first encountered at test.

Discriminative training is usually undertaken with CS+ and CS- presentations intermixed, and reduces generalization from CS+ to CS-, compared to a situation in which only CS+ is trained and CS- first encountered at test. The effect of this procedure on stimulus discrimination has been documented in numerous species including dogs (Pavlov, 1927), pigeons (Jenkins & Harrison, 1960, 1962), goldfish (Ames & Yarczower, 1965), rats (Rescorla, 1976; Yerkes & Dodson, 1908), and humans (Baron, 1973). The effect appears to be general across different learning procedures (Pavlovian and instrumental, aversive and appetitive) and CS/US types.

Evidence for the effect of differential training on discrimination is often embedded in tests of generalization along a dimension, which typically find a sharpening of the generalization gradient (i.e., stronger discrimination) for values between the CS+ and the CS- (e.g., see evidence from pigeon studies reviewed by Ghirlanda & Enquist, 2003, Test 12).

3.2 Positive patterning (AA)

After training with intermixed presentations of a compound of two stimuli followed by an outcome (AB+) and presentations of each of the two individual stimuli followed by no outcome (A-, B-), responding to the compound is stronger than responding to the individual stimuli.

First reported by Pavlov (1927), acquisition of a positive patterning discrimination has been widely documented in multiple species including dogs (Woodbury, 1943), honeybees (Deisig et al., 2001), rabbits (e.g., Bellingham et al., 1985), rats (e.g. Rescorla, 1972) and humans (e.g., Lachnit & Kimmel, 1993; Young et al., 2000), using Pavlovian (e.g., eyeblink conditioning, appetitive approach, autonomic conditioning, human predictive learning) and instrumental learning procedures.

Compared to other conditional discriminations (i.e., those in which the outcome associated with a stimulus compound does not follow simply from the outcomes paired with the individual stimuli), positive patterning is characterized by relatively fast acquisition and more frequent incidence of successful discrimination. Reports of groups of animals consistently failing to acquire positive patterning are virtually non-existent.

3.3 Asymmetry in intensity/magnitude discrimination (AA)

When a discrimination (A+, B-) involves stimuli that differ in intensity or magnitude, acquisition is faster when A+ is more intense or greater in magnitude.

Following discrimination training with two stimuli on the same dimension where A is of greater intensity (e.g., louder tone) or magnitude (e.g., more dots) than B, the discrimination is acquired more readily if the CS+ is of greater magnitude/intensity than the CS- (A+/B- is learned faster than B+/A-).

A review by Inman and Pearce (2018) concluded that the asymmetry in discrimination when two stimuli lie on the same intensity dimension is both “robust and

of considerable generality”. Intensity/magnitude effects have been found with a variety of species (rats, bees, and pigeons), USs (aversive and appetitive), stimulus dimensions (auditory volume, tone intensity, odor intensity, duration, and magnitude), and in both Pavlovian and instrumental procedures. There have also been some demonstrations in humans (Astley et al., 2015; Moore, 1964).

There is some evidence that intensity effects differ from magnitude (i.e., quantity) effects. Magnitude effects appear to be moderated by what is presented in the intertrial interval (ITI), while intensity effects are not (Inman & Pearce, 2018). The magnitude asymmetry is eliminated if the ITI is removed, or if a stimulus of high magnitude is presented in the ITI (Inman et al., 2016).

3.4 Negative patterning (A)

After training with intermixed presentations of two individual stimuli followed by an outcome (A+, B+) and a compound of those two stimuli followed by no outcome (AB–), responding to the individual stimuli is stronger than responding to the compound.

Domains: Widely observed but unclear impact of procedural variations

First reported by Pavlov (1927), acquisition of a negative patterning discrimination has been documented in numerous species, including dogs (Woodbury, 1943), rats (Rescorla, 1972; Whitlow & Wagner, 1972), rabbits (Bellingham et al., 1985), bees (Deisig et al., 2001), and humans (Lachnit & Kimmel, 1993; Lachnit et al., 2008; Livesey, Thorwart, & Harris, 2011a), using Pavlovian (e.g., eyeblink conditioning, fear conditioning, human predictive learning) and instrumental learning procedures.

Evidence for a general capacity to acquire negative patterning discriminations in laboratory animals is very strong. Despite this widespread evidence, some constraints on this capacity have also been reported. In rabbit eyeblink conditioning, Kehoe and Graham (1988) found that acquisition of negative patterning required relatively long CS durations,

with a consistent failure to learn the discrimination evident at the shortest (300 ms) CS duration. In honeybees, Deisig et al. (2007) found that negative patterning emerged only with longer ITIs, whereas bees consistently failed to acquire negative patterning under other conditions (Deisig et al., 2002, 2007). Also, some human conditioning studies did not observe negative patterning (Lachnit & Kimmel, 1993).

The learning of a negative patterning discrimination often involves an initial period in which responding to the compound is greater than to the individual cues (i.e., summation of responding), followed by a steady decline in responding to the compound to levels well below that elicited by the individual cues. This transition has been observed in rats, rabbits, and in some human experiments (Bellingham et al., 1985; Thorwart et al., 2017).

3.5 Positive patterning is easier than negative patterning (A)

Given a discrimination in which the compound of two stimuli (AB) is followed by a different outcome than the two stimuli individually (A, B), the learner acquires the discrimination faster when the compound predicts the US (positive patterning) than when the compound predicts the absence of the US (negative patterning).

See benchmark 3.2 for positive patterning, and 3.4 for negative patterning.

Domains: Widely observed but unclear impact of procedural variations

The difference in acquisition rates for positive and negative patterning has been observed across various Pavlovian and instrumental learning tasks in several species including rabbits (Bellingham et al., 1985), rats (Delamater et al., 2017; J. A. Harris et al., 2008), honeybees (Deisig et al., 2002, 2007), and humans (Lachnit & Kimmel, 1993; Livesey, Thorwart, & Harris, 2011b; Thorwart et al., 2017).

There are a few counterexamples where positive and negative patterning appear to be acquired at roughly the same rate, in human causal learning (Shanks & Darby, 1998;

Young et al., 2000) and other species (Rescorla, 1972; Woodbury, 1943). Bellingham et al. (1985) found that rats initially acquired positive patterning and negative patterning at the same rate, but when the discriminations were reversed, rats initially trained on a positive patterning schedule and switched to negative patterning displayed considerably greater difficulty acquiring the reversal discrimination than rats initially trained on negative patterning and then switched to positive patterning.

3.6 Biconditional discrimination (A)

After training with intermixed presentations of stimulus compounds in which no single stimulus signals the presence or absence of the outcome but each compound predicts the presence or absence of the outcome (AB+ / BC- / CD+ / AD-), responding is higher for the compounds that predict the outcome.

Domains: Widely observed but unclear impact of procedural variations

A biconditional discrimination is typically one in which no individual feature is a uniquely strong predictor of the outcome; thus, differential responding to individual stimuli is not expected based on any given feature in isolation. Rather, each configuration of stimuli signals the presence or the absence of the outcome.

Learning of biconditional discriminations has been reliably observed across various Pavlovian and instrumental learning tasks in several species including mice (Gonzalez et al., 2013; Ramirez & Colwill, 2012), pigeons (Rescorla et al., 1985), rabbits (Saavedra, 1975), rats (J. A. Harris et al., 2008; Lashley, 1938), and humans (J. A. Harris & Livesey, 2008; Lober & Lachnit, 2002).

However, some studies have not observed acquisition of the discrimination, indicating that the boundary conditions are not fully known (e.g. see Delamater et al., 2017).

3.7 Biconditional is harder than component discrimination (A)

Discriminative responding between the outcome-present and outcome-absent trials of a biconditional discrimination (AB+ / BC- / CD+ / AD-) is slower than discriminative responding between the outcome-present and outcome-absent trials of a component discrimination that is matched for complexity but in which single stimuli signal the presence or absence of the outcome (AB+ / BC- / CD- / AD+).

Domains: Appetitive Pavlovian and instrumental conditioning, human causal learning

While many animals can learn biconditional discriminations (see benchmark 3.6), they are acquired more slowly than component discriminations. The term *component discrimination* is mainly used in the context of biconditional discriminations and is rarely regarded as interesting in its own right. The difference in rate of acquisition of biconditional versus matched component discriminations has been found in appetitive Pavlovian and instrumental conditioning in several species, including rabbits (Saavedra, 1975), rats (Preston et al., 1986), and pigeons (Honig & Wasserman, 1981), as well as human causal learning (Livesey et al., 2019; Livesey, Thorwart, De Fina, et al., 2011).

Typically, direct comparisons between these discriminations involve a component discrimination that is matched to the complexity of the biconditional discrimination; both discriminations involve presentations of pairs of stimuli, two of which are reinforced and two of which are non-reinforced. However, only the component discrimination is a linearly separable problem in the sense that a single stimulus consistently signals the presence of the outcome and another consistently signals its absence. The effect does not appear to be stimulus-specific and has been found using combinations of discrete cues as well as combinations of a single discrete cue and a distinct context (Preston et al., 1986). Direct comparisons between biconditional and component discriminations, matched in

this way, are not common in the literature on biconditional discriminations, but to our knowledge, there are no published observations to the contrary, suggesting the relative difficulty is consistent.

3.8 Simultaneous feature-positive discrimination (A)

Simultaneous presentations of two stimuli paired with a US (AX+), intermixed with presentations of one stimulus with no US (X-), result in stronger responding to the compound (AX) than to the single stimulus (X) alone, and strong responding in the presence of the other stimulus (A).

Domains: Observed in multiple procedures across species, but not universal

See the closely related feature discrimination benchmarks 3.9-3.11 and 3.16

In feature discriminations, the stimulus presented alone (X) is commonly termed the *target*, and the other stimulus (A) is termed the *feature*. Thus, simultaneous feature-positive discrimination results when a feature-target compound (AX) is reinforced and the target on its own is not. Simultaneous feature-positive discriminations are readily acquired in animal species including pigeons (Jenkins, & Sainsbury, 1969), rats (Reberg & Leclerc, 1977) and humans (Newman et al., 1980), encompassing Pavlovian and instrumental as well as aversive and appetitive procedures. In relation to serial feature-positive discrimination (see benchmark 3.9), there are a number of differences (for reviews, see Fraser & Holland, 2019; Holland, 1992). For example, the CR to the compound AX resembles that evoked by the feature (A) and not the target (X). Further, in tests of summation, the feature will summate but not the target. Finally, extinction of the feature will significantly impair responding on AX+ trials (although there is evidence to the contrary in humans, Baeyens et al., 2001a). Together, this suggests that the discrimination is solved by direct conditioning of the feature to the outcome, and not by modulating the association between the target and its outcome.

It is important to note that, in a preparation used primarily by Bonardi in which the feature is long-lasting with intermittent presentations of the target within it, in some cases the feature can acquire properties that are more frequently observed in serial presentations (Bonardi, 1992; Bonardi et al., 2017).

3.9 Serial feature-positive discrimination (A)

Serial presentations of two stimuli paired with the US (A->X+), intermixed with presentations of one stimulus with no US (X-), result in stronger responding to the compound (A->X) than to the single stimulus (X) alone, but minimal responding in the presence of the other stimulus (A).

Domains: Appetitive Pavlovian conditioning in pigeons and rats, appetitive instrumental conditioning in rats, rabbit eyeblink conditioning, human conditioned suppression

See the closely related feature discrimination benchmarks 3.8, and 3.10-3.12

In serial feature-positive discriminations, the feature A is presented before the target X in a non-overlapping manner. This is also termed *positive occasion setting*. Serial feature-positive discriminations are very robust and have been observed across species including rabbits (Moore et al., 1969), pigeons (Looney & Griffin, 1978), rats (Ross & Holland, 1981) and humans (Baeyens et al., 2001b). While the effect has mainly been investigated in appetitive (Pavlovian and instrumental) procedures (for a review, see Fraser & Holland, 2019), there are also examples with aversive US (Baeyens et al., 2001b; Moore et al., 1969).

In relation to simultaneous feature-positive discrimination (see benchmark 3.8), the CR to the compound X resembles what would have been evoked by the target (A) alone, and not the feature (A) (for reviews, see Fraser & Holland, 2019; Holland, 1992). The ability of the feature (A) to modulate responding to its target (X) does not readily

transfer to other CSs, is immune to counterconditioning, and acts to enhance the response form elicited by the target (Baeyens et al., 2001a; for reviews, see Fraser & Holland, 2019; Holland, 1992). The magnitude of serial feature-positive discriminations at test is dependent on the ISI between the feature and the target as well as between the target and US used in training (Holland, 1992, 1998b; Holland et al., 1997). These discriminations are generally strongest if the feature and target are of different stimulus modalities, and when the target is more intense (e.g. louder, brighter, more concentrated than the feature; Fraser & Holland, 2019).

3.10 Simultaneous feature-negative discrimination (A)

Presentations of one stimulus paired with a US (X+) intermixed with simultaneous presentations of two stimuli without the US (AX-), result in stronger responding to the single stimulus (X) alone than to the compound (AX), while the other stimulus (A) acquires the ability to suppress responding when combined with another stimulus that has been paired with the outcome.

Domains: Observed in multiple procedures across species, but not universal

See the closely related feature discrimination benchmarks 3.8-3.9, 3.11 and 3.16.

Simultaneous feature-negative discriminations result from a procedure in which the feature-target compound AX is not reinforced, while the target X on its own is. This phenomenon describes the acquisition of this discrimination (see conditioned inhibition, benchmark 5.1, for a procedure that involves similar training but a different test).

Simultaneous feature-negative discriminations are acquired in animal species including pigeons (Jenkins, & Sainsbury, 1969), rats (Reberg & Leclerc, 1977) and humans (Fiedler et al., 1989) encompassing Pavlovian and instrumental as well as aversive and appetitive procedures; although they appear to be harder to learn, compared to feature-positive discriminations (see feature-positive effect, benchmark 3.16).

In relation to serial feature-negative discrimination (see benchmark 3.11), there are some differences (Baeyens et al., 2004b; for reviews, see Holland, 1992; Fraser & Holland, 2019). For example, the feature readily transfers and acts as an inhibitor for novel compounds. After training, acquisition of direct associations between the feature and an outcome is slowed relative to control cues, suggesting they already had acquired inhibitory associative strength. Finally, counterconditioning of the feature will significantly affect responding on AX- trials and actually result in summation (greater responding than to X+ alone, Holland, 1984c, 1989). This is often interpreted as suggesting that the simultaneous discriminations are solved by direct inhibitory conditioning of the feature to the outcome, and not by modulating the association between the target and its outcome.

3.11 Serial feature-negative discrimination (A)

Presentations of one stimulus paired with a US (X+) intermixed with serial presentations of two stimuli without the US (A->X-), result in stronger responding to the single stimulus (X) alone than to the compound (A->X), but the other stimulus (A) does not acquire the ability to suppress responding when combined with another stimulus that has been paired with the outcome B+.

Domains: primarily appetitive conditioning

See the closely related feature discrimination benchmarks 3.8-3.10 and 3.12

Serial feature-negative discriminations have been observed across species and procedures including conditioned suppression in rats (Holland, 1984a, 1989) and humans (Baeyens et al., 2004a), pigeon autoshaping (Rescorla, 1985), and conditioned taste avoidance in rats (Huang et al., 2023).

A common aspect of serial feature negative discriminations is that the ability of the feature (A) to modulate responding to its target cue (X) does not readily transfer to a

different CS, is immune to counterconditioning, and does not result in slowing of acquisition of direct associations between the feature and an outcome relative to an untrained cue (Fraser & Holland, 2019; Holland, 1992). The magnitude of serial feature-negative discriminations is dependent on the ISI between the feature and the target as well as between the target and US (Holland, 1992). These discriminations are generally best observed if the feature and target are of different stimulus modalities and when the target is more intense (e.g., louder, brighter, more concentrated) than the feature.

One potential boundary condition is that the acquisition of a serial feature-negative discrimination is impaired in adolescent rats who also do not exhibit immunity to counterconditioning (Meyer & Bucci, 2017). In humans trained with a conditioned suppression procedure, there is evidence that counterconditioning of the feature can disrupt occasion setting in serial preparations (Baeyens et al., 2004b). Whether this is driven by the precise procedures used or is representative of these processes in humans remains to be determined.

3.12 Resistance of occasion setting to extinction and counterconditioning (A)

After serial feature-positive or feature-negative discrimination, the ability of the feature to disambiguate the target is resistant to extinction and counterconditioning.

Domains: Appetitive and aversive Pavlovian conditioning in rats

See the closely related feature discrimination benchmarks 3.9 and 3.11

When trained in a serial feature-positive or feature-negative discrimination (see benchmarks 3.9, 3.11), the ability of the feature to disambiguate the target is resistant to extinction and counterconditioning, respectively. This is often taken to suggest that the propensity of features in these discriminations to affect the associative relationship between a target and an outcome is independent of any simple conditioning to the feature or relationship between the feature and an outcome (Fraser & Holland, 2019; Morell &

Holland, 1993), although the two effects do not appear to be mutually exclusive. In some cases, these discriminations can mimic patterning preparations (Woodbury, 1943).

There is strong evidence that, for serial feature-positive discriminations, non-reinforcement of the feature (A-) has no impact on the acquisition or expression of the discrimination. This can occur either during acquisition (A-; X-; AX+) in a manner analogous to positive patterning, or separately after acquisition (Fraser & Janak, 2019; Ross & Holland, 1982). In serial feature-negative preparations, with either food or shock as the outcome, there is no impact of reinforcement of the feature on its ability to disambiguate the target as not leading to reinforcement (Holland, 1984b). The same procedures in simultaneous discriminations abolish the ability of A to disambiguate the relationship between X and reinforcement (for a review, see Fraser & Holland, 2019).

Little to no evidence exists to suggest that counterconditioning generalizes across domains (e.g., when A indicates X will be followed by food, the ability of A to disambiguate X is preserved if A is directly associated with shock). In humans, there is one report that counterconditioning of the feature in a serial feature-negative discrimination using a conditioned suppression procedure (Baeyens et al., 2004b) abolished its ability to disambiguate its target. Whether this is a species-specific effect within feature-negative discriminations requires future investigation.

4 Extinction

In this section, we discuss the effect of procedures that reduce the CR after initial acquisition.

4.1 Extinction (AA)

The CR decreases when CS-US pairings are followed by presentations of the CS alone or by unpaired CS and US presentations.

Extinction refers to reduction in intensity, strength, or frequency of the CR as a result of the repeated non-reinforced CS presentations. Complete extinction would be achieved when the CR returns to its pre-acquisition baseline. Extinction was first described by Pavlov (1927) and has since been demonstrated across a wide variety of species (including humans, rodents, dogs, snails, *Aplysia*, and others) and learning domains (Pavlovian/instrumental, appetitive/aversive), using a very wide variety of CRs and instrumental responses (for authoritative reviews, see Delamater, 2004; Myers & Davis, 2002; Rescorla, 2001).

Extinction is so general and ubiquitous that it is rarely the subject of dedicated study. Most research on extinction is performed in the context of manipulations that are expected to hamper or enhance extinction learning (e.g., the partial reinforcement extinction effect, see benchmark 4.6) or to cause a recovery of conditioned responding after extinction (e.g., renewal, reinstatement, and spontaneous recovery, see benchmarks 4.3, 4.4, 4.8, 4.9, 4.17).

One type of learning that some have argued to be relatively insensitive to extinction is evaluative conditioning, that is, the learning of likes and dislikes of cues as a result of pairings with USs. However, the degree to which evaluative conditioning is qualitatively different in this regard from other forms of associative learning remains contested (Hofmann et al., 2010). Another potential boundary condition on extinction concerns the immediate extinction deficit, which refers to the observation that extinction trials that are administered immediately after conditioning may have only minimal effect (Maren, 2014). This phenomenon is probably specific to fear conditioning, however, and may relate to the negative effects of acute stress on the encoding and retrieval of extinction memories.

4.2 Counterconditioning (AA)

CS–US training with an aversive US diminishes an appetitive CR otherwise produced by prior CS–US training with an appetitive US (and conversely).

See Table S2.

Counterconditioning refers to both a procedure and a phenomenon (Keller et al., 2020). In the procedure, a CS initially paired with a US1 in phase 1 is now coupled with a new US2 of opposing valence (Jones, 1924). As a phenomenon, the initial CR acquired in phase 1 is reduced by the counterconditioning procedure in phase 2. The earliest demonstration was the “Little Peter” experiment by Mary Cover Jones (1924), in which a child’s fear of certain stimuli (e.g., a rabbit) was reduced through counterconditioning.

To demonstrate counterconditioning, it is common to compare the CR during or after counterconditioning with the CR during or after initial acquisition. In this sense, counterconditioning is similar to extinction: the CR is diminished when a CS is no longer paired with the (initial) US. A second contrast sometimes employed is to compare counterconditioning (CS is coupled with a new US2) to extinction (CS is coupled with no US).

Using the first comparator, counterconditioning has been widely demonstrated in humans (including children) and rats, across a range of CSs (tones, a black compartment, steady lights, neutral human faces, fear-relevant images, serving trays, etc.), aversive USs (foot shock, white noise, electric shock, bitter-tasting liquids, etc.), appetitive USs (food pellets, maltose, sucrose, yellow rubber ducks, baby laughs, cartoon images, funny film clips, monetary reward, chocolate, etc.), CRs (freezing, head-jerks, magazine entries, time spent in a threatening location, skin conductance responses, heart rate, CS valence, US expectancy, etc.), procedures (Pavlovian aversive-to-appetitive and appetitive-to-aversive conditioning, instrumental aversive-to-appetitive conditioning), and

laboratories (Keller et al., 2020). Boundary conditions and moderators have been proposed, but none of these have been independently replicated (Keller et al., 2020).

Using the second comparator, there is much less evidence to suggest that counterconditioning leads to faster diminution of the CR than extinction. Faster decrement of the CR has been demonstrated in rats and humans, mostly for aversive-to-appetitive counterconditioning, but with (a) no robust report for appetitive-to-aversive counterconditioning (see supplementary table and Keller et al., 2020), and (b) a considerable number of null and even opposing results (i.e., extinction is more effective in diminishing the CR than counterconditioning), overall comprising around one-third of the published experiments on the issue. In light of these discrepancies, one report that ABA and ABC renewal (see benchmarks 4.3-4.4) after aversive-to-appetitive counterconditioning in rats are more pronounced than after extinction (Holmes et al., 2016) would also appear to require further support.

4.3 ABA renewal (AA)

If CS-US acquisition takes place in context A and extinction in context B, then testing the CS in context A produces a stronger CR than in context B.

Classically, a CR at test (without the US) in an ABA group is compared to a CR in an AAA control group that receives acquisition, extinction and testing all in context A. The return of the CR under these conditions was first discovered in a conditioned suppression preparation in rats (Bouton & Bolles, 1979) and later widely replicated with different responses (e.g., freezing), with different types of contexts (e.g., rooms in a virtual reality environment), in different learning domains (classical/instrumental, appetitive/aversive) and different species (rats, mice, and humans). More recent studies of ABA renewal use an ABB control, as in the procedure described above, so that the only difference between the renewal and control condition is the context of testing. ABA

renewal is thus a very robust and widely replicated phenomenon (for reviews, see Bouton et al., 2021; Wang et al., 2024).

ABA renewal is commonly interpreted as evidence that extinction does not reflect “unlearning” of previously acquired CS—US contingency knowledge, but rather the acquisition of supplementary information that co-exists and competes with the previously acquired knowledge (Pavlov, 1927). However, the basic demonstration of ABA renewal relative to its typical AAA or ABB control condition leaves room for various alternative explanations (for an overview, see Vervliet, Baeyens, et al., 2013). Several additional controls have therefore been considered in follow-up work.

In particular, responses measured to the CS may be influenced by learning of an excitatory association to context A or an inhibitory association to context B. There is some evidence against excitatory conditioning of context A from fear conditioning in rats, but there is little conclusive evidence in instrumental conditioning preparations with rodents, or with humans (Vervliet, Baeyens, et al., 2013). There is some evidence against inhibitory learning to context B in fear conditioning studies in rats (Bouton & King, 1983). However, this extra test has rarely been applied in other experimental setups and species.

In conclusion, the ABA renewal procedure robustly yields a return of conditioned responding to a CS after extinction. However, ruling out any potential contribution of excitatory or inhibitory learning to contexts A or B relies on additional criteria that are much less robustly established across species and response systems.

4.4 ABC renewal (AA)

If CS-US acquisition takes place in context A and extinction in context B, then testing in novel context C produces a stronger CR to the CS than in context B.

Typically, a CR at test in an ABC group is compared to a CR in context B in an ABB control group (as in benchmark 4.3 above), or alternatively with an AAA control group

that receives acquisition, extinction, and testing all in context A. The return of conditioned responding under these circumstances was first discovered in a conditioned suppression preparation in rats (Bouton & Bolles, 1979), and further investigated with different responses (e.g., freezing), types of contexts (e.g., rooms in a virtual reality environment), learning domains (classical/operant, appetitive/aversive), and species (mice, rats, and humans). Although ABC renewal has been robustly demonstrated in extinction research, it has received much less attention than its most widely investigated counterpart, ABA renewal (Bouton et al., 2021) – see benchmark 4.3.

Like other forms of renewal, ABC renewal is commonly interpreted as evidence for lingering CS-US contingency knowledge after extinction (Pavlov, 1927) but leaves room for various alternative explanations (for an overview, see Vervliet, Baeyens, et al., 2013). Several additional controls have therefore been considered in follow-up work.

In particular, responses measured to the CS may be influenced by inhibitory learning to context B, unconditioned responding to context C, or a change in perception of the CS in moving from context A to context B. There is evidence against this last idea from fear conditioning in rats, but less so in the case of operant conditioning setups (Bouton et al., 2021) or in humans (Vervliet, Baeyens, et al., 2013). There is some evidence against inhibitory learning to context B in fear conditioning studies in rats (Bouton & King, 1983). However, this extra test has rarely been applied in other experimental procedures and species. The possibility of unconditioned responding to context C has been suggested in some human studies (Effting & Kindt, 2007).

In conclusion, ABC renewal is a robust procedure to elicit a return of conditioned responding after extinction, but its theoretical analysis in terms of the contextual specificity of extinction learning rests on additional criteria that are much less robustly established across species and response systems.

We suggest that this theoretical ambiguity might have contributed to the wide distribution of grades in the survey (with equal numbers of the extreme grades AA and C), resulting in a median grading of B.

4.5 Protection from extinction (A)

After pairing stimulus A with a US, and conditioned inhibition training with stimulus B, presenting AB-noUS compounds leads to a higher CR to A alone, compared to conventional extinction (A-noUS presentations).

Domains: Pavlovian aversive and appetitive conditioning in rats, pigeons, humans

Protection from extinction was first predicted by Konorski (1948) and experimentally established by Soltysek and Wolfe (1980) in a fear conditioning setup in cats. The first demonstration within human fear conditioning was obtained by Lovibond (2000a). Although protection-from-extinction has not been studied very often, the available studies (e.g., McConnell & Miller, 2010; Rescorla, 2003) show that the increase in CR strength during test is rather robust across CRs (leg flexion, conditioned suppression, SCR, causal judgment), learning systems (appetitive and aversive), and species (rats, pigeons, humans). Whether the observed increase in the CR after combined extinction is due to the inhibitory properties of the conditioned inhibitor, however, is less clear. Some studies find the same effect when an excitatory stimulus instead of a stimulus trained as an inhibitor is added (Lovibond et al., 2000b; Vervliet et al., 2007).

4.6 Partial-reinforcement extinction effect (A)

Extinction is slower following partial rather than continuous reinforcement.

Domains: Domain-general with short ITI and between-subjects tests

The first systematic demonstration of the partial-reinforcement extinction effect (PREE) dates back at least 85 years (Humphreys, 1939). The PREE has since been

demonstrated widely in humans (including children), rats, pigeons, toads and goldfish, most often in appetitive preparations but also in aversive (notably fear conditioning) procedures (for reviews, see Amsel, 1992; Mackintosh, 1974). Initially, it was believed that the PREE was robustly observed only in instrumental learning, but the phenomenon has now been firmly established in classical conditioning procedures as well (e.g., Pearce et al., 1997).

Whereas the PREE is readily observed in between-subject procedures (comparing groups that typically received the same number of USs in a continuous versus partial reinforcement schedule during acquisition), results in within-subjects procedures are more variable, with some yielding a similar PREE as in between-subjects procedures (e.g., Chan & Harris, 2019; Rescorla, 1999) but others yielding a reversed PREE (i.e., faster extinction for a CS that inconsistently signalled the US; e.g., Pearce et al., 1997; Svartdal, 2000). Another widely documented boundary condition concerns the use of massed versus spaced trials (i.e., greatly increasing the time interval between trials may abolish or even reverse the PREE; Papini et al., 2002). The PREE may also be reduced when a delay is inserted between acquisition and extinction training (Norton & Harris, 2022).

4.7 Contingency degradation (A)

Interspersing unsignalled US presentations during CS-US acquisition reduces the CR.

Domains: Domain-general, across several species including rats, mice, pigeons, and humans; but not demonstrated universally

Contingency degradation (CD) refers to the attenuation of the CR resulting from the addition of *unsignalled* US presentations interspersed among CS-US pairings. Similarly, in instrumental procedures, inserting *non-contingent* USs during instrumental training reduces the rate or vigor of instrumental responding.

The contingency degradation effect was first reported in a Pavlovian fear conditioning procedure in rats by Rescorla (1968) who demonstrated that the magnitude of the CR was proportional to the contingency between the CS and the US. Equal probability of a shock US in the presence and absence of the CS prevented the development of a conditioned fear response to the CS, whereas the same probability of shock in the presence of the CS in combination with a zero-probability of shock in the absence of the CS promoted strong conditioned fear responding to the CS. Contingency degradation in Pavlovian fear conditioning procedures has been widely replicated (e.g., Durlach, 1983; Urcelay & Miller, 2006b; Witnauer & Miller, 2007).

Contingency degradation effects have also been demonstrated in appetitive Pavlovian procedures (Murphy & Baker, 2004), in instrumental learning procedures (Balleine & Dickinson, 1998; Colwill & Rescorla, 1986; e.g., Gamzu & Williams, 1973), as well as in a variety of species other than rats including pigeons (e.g., Gamzu & Williams, 1973), mice (e.g., Qian et al., 2024) and humans (e.g., Dickinson et al., 1984; Morris et al., 2022). While the role of contingency as a necessary and/or sufficient factor for learning remains contested (see Papini & Bitterman, 1990), the basic observation that adding unsignalled USs reduces CR strength, relative to a situation in which no unsignalled USs are administered, appears to be general and robust.

An important boundary condition is that administering unsignalled USs *after* CS-US training often does not weaken the degree of conditioned responding to the CS, unlike adding unsignalled USs *during* CS-US training as in CD, or before acquisition as in the US pre-exposure effect (benchmark 7.1) (for discussion, see Hallam et al., 1992).

4.8 Spontaneous recovery (A)

Presentation of the CS some time after successful extinction partially restores the CR.

Domains: Domain-general in rodents and humans, but not universal

Spontaneous recovery refers to the partial return of the CR as a function of the mere passage of time after successful extinction training, in the absence of any other experimental manipulations. The phenomenon was first described by Pavlov (1927) and in the context of examining the learning mechanisms engaged during extinction after Pavlovian acquisition (for a review and summary see Rescorla, 2004). Spontaneous recovery has been reported in appetitive and aversive Pavlovian procedures in species including rabbits, pigeons, rats, and humans, and has occasionally also been reported after instrumental conditioning (Rescorla, 1997a).

In one study with rats, the level of CRs 6 days after extinction was equal to the level of CRs at the end of acquisition training (Brooks & Bouton, 1993). Spontaneous recovery appears to decrease with increasing amounts of extinction training (Rescorla, 2004). The degree of spontaneous recovery has been shown to be related to the length of the extinction training-test time interval (Quirk, 2002), resulting in higher levels of the CR as more time passes. Consequently, the investigation of spontaneous recovery in a strict sense requires multiple test time points to map the return of the CR as a function of time. This is typically what is procedurally done in rodents, comparing different experimental groups (Rescorla, 2004). In human studies, however, the spontaneous recovery test is typically identical to the extinction training phase and a single time interval is used, which varies between 24 and 94 h depending on the study (Vervliet, Craske, et al., 2013). In humans, to date no systematic investigations or meta-analyses on the role of different extinction training-to-test intervals are available. In addition, rodent as well as human studies have reported inconsistent evidence on the role of the timing of extinction relative to acquisition training for the expression of spontaneous recovery (Alvarez et al., 2007; Myers et al., 2006; Rescorla, 2004).

Spontaneous recovery is typically inferred by comparing the CR at the end of the extinction session with the beginning of a later test session in rodents (Rescorla, 2004) and humans (Lonsdorf et al., 2017). The challenges of such comparisons have been highlighted for outcome measures that are subject to strong habituation over time (Lonsdorf et al., 2017). Nonetheless, studies that addressed these issues found clear evidence for spontaneous recovery beyond habituation and other non-associative factors (e.g., Quirk, 2002).

5 Inhibitory conditioning

As several benchmarks in this section are closely related to each other and use similar tests, we introduce them in this opening commentary. In general, conditioned inhibition refers to the behavioral control by a CS (the putative inhibitory conditioned stimulus) after it has been trained on an objective negative correlation with a US. A negative CS-US correlation can be established through several different procedures, each described as a separate phenomenon: simultaneous feature-negative discrimination, negative contingency training, and differential conditioning (for reviews of the construct of conditioned inhibition, see Savastano et al., 1999; Sosa & Ramírez, 2019).

The behavioral impact of the CS can be assessed by several different means. In a summation test, the putative inhibitor, CS A, is presented in compound with another CS B that previously has been paired with the US on separate trials; A is regarded as a conditioned inhibitor if responding during the AB compound is weaker than the response elicited by B alone or B in compound with an affectively neutral stimulus without a conditioning history. In a retardation test, A is repeatedly paired with the US to establish excitatory conditioned responding to A, which should require more A-US pairings compared to equivalent response acquisition in a control condition lacking the negative correlation training treatment with A. As passing the summation test for inhibition could

be confounded by initial training having increased attention to A, and passing the retardation test for conditioned inhibition could be confounded by initial training having decreased attention to A, the usual standard for A to be regarded as a conditioned inhibitor is passing both the summation and the retardation test (Rescorla, 1969b). The two tests for conditioned inhibition usually result in convergent results.

5.1 Conditioned inhibition after simultaneous feature-negative discrimination (A)

After interspersed AB-noUS presentations and B-US pairings, A reduces the CR when paired with a US-predictive C (summation test), and when A is paired with the US, acquisition of a CR is retarded (retardation test).

Domains: Multiple Pavlovian conditioning domains, but not universal

In simultaneous feature-negative discrimination, also referred to as Pavlov's procedure for conditioned inhibition training, A becomes a signal for the absence of the US when it is otherwise expected.

Conditioned inhibition revealed in a summation test following this procedure has been documented, for example, in dogs using salivary conditioning (Pavlov, 1927), and rats using eyeblink conditioning and conditioned lick suppression (Urcelay & Miller, 2006a). In humans, it has been observed with various testing preparations, including skin conductance conditioning (R. J. McNally & Reiss, 1982), predictive learning (Melchers et al., 2006), and evaluative conditioning (Thurston & Cassaday, 2015). Moreover, the training procedure has proven effective even with invertebrates (e.g., appetitive conditioning in snails, Acebes et al., 2012).

Conditioned inhibition revealed by retarded response acquisition following simultaneous feature-negative discrimination has been observed, for example, with eyeblink conditioning (Campolattaro et al., 2008) and conditioned lick suppression

(Urcelay & Miller, 2006a) preparations in rats, in human evaluative learning (Thurston & Cassaday, 2015), and appetitive conditioning in snails (Acebes et al., 2012).

For both measures, conditioned inhibition after simultaneous feature-negative discrimination training appears more likely with spaced rather than massed trials (Urcelay & Miller, 2006a). Moreover, the simultaneous nature of the feature-negative discrimination seems to be relevant, as conditioned inhibition is less likely with a sequential procedure in which A precedes B in the compound trials (for a review, see Swartzentruber, 1995).

An asymmetry is often seen between excitatory and inhibitory conditioning, with inhibitory conditioning (AB-noUS) proceeding slower (i.e., taking more trials), potentially because its acquisition appears to be dependent on the excitatory conditioning (B-US) with which it is contrasted during training (J. A. Harris et al., 2016).

5.2 Conditioned inhibition after negative contingency training (A)

After interspersed A-noUS and unsignalled US presentations, A reduces the CR when paired with a US-predictive B (summation test), and when A is paired with the US, acquisition of a CR is retarded (retardation test).

Domains: Multiple Pavlovian conditioning domains, but small effect size suggests heterogeneity between individuals.

After negative contingency training, conditioned inhibition has been revealed through a summation test using, for example, a conditioned suppression procedure with rats (Droungas & LoLordo, 1995; Rescorla, 1969a). Evidence for retarded acquisition after negative contingency training is seen, for example, in conditioned suppression in rats (Droungas & LoLordo, 1995; Rescorla, 1969a), autoshaping in pigeons (Hearst & Franklin, 1977), and human contingency judgements (Chapman & Robbins, 1990). The phenomenon is widely reported, but the effect size is usually small, suggesting the

phenomenon is heterogenous between individuals, and/or small in relation to the heterogeneity in the CR.

6 Stimulus competition/potentiation

In this section, we discuss benchmarks relating to learning about multiple CS embedded in a regularity with a single US.

6.1 Overshadowing (A)

Conditioning to the compound AB results in a weaker CR to B than is attained with B-US pairings.

Domains: Several Pavlovian conditioning tasks across domains and species with well-known boundary conditions, but the opposite effect (potentiation) is sometimes observed for reasons not yet fully characterized.

Overshadowing was reported by Pavlov (1927) using salivary conditioning in dogs and later observed in visual-discrimination learning by fish (Tennant & Bitterman, 1975), eyeblink conditioning in rabbits (Kehoe, 1982), conditioned suppression in rats (Blaisdell et al., 1998), freezing in rats (G. P. McNally & Westbrook, 2003), and spatial learning in rats (Pearce et al., 2006) as well as human contingency judgements (Price & Yates, 1993).

Boundary conditions for overshadowing include (1) the number of AB-US compound conditioning trials - overshadowing can be seen with a single trial (e.g., Mackintosh & Reese, 1979) and weakens across repeated compound stimulus presentations (Bellingham & Gillette, 1981); (2) sensory modality, with overshadowing weaker or absent when A and B are from the same or similar modalities (Durlach & Rescorla, 1980); (3) the saliency of A and B as assessed by independent rates of acquiring CRs (Mackintosh, 1976), with overshadowing of the less salient cue most commonly observed and reciprocal overshadowing of the more salient cue less commonly observed;

and (4) temporal and spatial contiguity between A, B and the US (Herrera et al., 2022), with overshadowing more pronounced with greater contiguity.

Potentiation is the inverse result of the same procedure as overshadowing, that is, a stronger CR to B than is attained with B-US pairings. Although infrequently observed, potentiation is most commonly seen when B is olfactory and A is gustatory in taste aversion learning in rats (Droungas & LoLordo, 1995; Rusiniak et al., 1979). It has also been reported with two gustatory cues (Bouton et al., 1987), auditory cues with conditioned suppression in rats (Urcelay & Miller, 2009), and spatial learning to escape water in rats (Pearce et al., 2006), as well as with B being visual and A being gustatory in taste aversion learning with rats (Galef & Osborne, 1978). Most reports of potentiation have come from studies using rats. It has also been observed in pigeons (Clarke et al., 1979), but it has not been seen in humans to date (Alcalá, Kirkden, et al., 2023). Potentiation appears more likely when the contiguity between the cues and outcome is weak with taste aversion in rats (Batsell et al., 2012).

6.2 Forward blocking (A)

Conditioning to a compound AB results in weaker conditioning to B when the former is preceded by conditioning to A than when it is not.

Domains: Frequently observed across species and conditioning tasks with well-known boundary conditions, but the opposite effect (augmentation) is sometimes observed for reasons not yet fully identified.

Blocking was first reported by Kamin (1968) using conditioned suppression in rats, and later in rats with conditioned freezing (G. P. McNally et al., 2004), rabbit eyeblink conditioning (Marchant et al., 1972), appetitive conditioning in rats (Holland, 1984d), autoshaping in pigeons (Khallad & Moore, 1996), conditioned proboscis extension in honeybees (B. H. Smith & Cobey, 1994), fish visual discrimination learning (Tennant &

Bitterman, 1975), rodent spatial learning (Rodrigo, 2002) and human causal learning (Beckers et al., 2005; Dickinson et al., 1984), among others. It has also been observed in instrumental procedures (Vandbakk et al., 2020).

Blocking, however, is not ubiquitous (Maes et al., 2016). Boundary conditions include (1) the number of AB-US compound conditioning trials, with blocking not always seen with a single AB-US trial (Dickinson et al., 1983) or with a relatively large number of trials (Azorlosa & Cicala, 1986); (2) US identity, with blocking weakened when training A-US1 and AB-US2 (Takahashi et al., 2017); (3) as a specific case of this, US valence, with blocking weakened by changes in US valence between the A and AB training (Dickinson, 1977); (4) spatial locus of US delivery between the A and AB training, with blocking weakened by changing the locus of the US (Betts et al., 1996; Stickney & Donahoe, 1983); (5) CS-US interval, with blocking reduced by a change in intervals (Dickinson et al., 1976); and (6) the number of blocking cues, with blocking reduced by an increase in the number of blocking cues (Witnauer et al., 2008).

Interestingly, in select circumstances, the same procedure results in stronger responding to B, that is, it has the opposite effect. This is referred to as *augmentation*, similar to potentiation (see benchmark 6.1). It has been reported in conditioned aversion with rats with odor as A and taste as B (Batson & Batsell, 2000), and taste as A and odor as B (Batsell et al., 2001), and in human contingency learning under time pressure (Vadillo & Matute, 2010). The boundary conditions for augmentation are yet to be established.

6.3 Superconditioning (A)

Reinforced AB presentations following inhibitory conditioning of A increase the CR to B as compared with when B is trained in the absence of A.

Domains: Varied Pavlovian conditioning procedures and species, but a limited number of demonstrations, and the potential boundary conditions are not known

Rescorla (1971) reported the superconditioning effect using conditioned suppression in rats, and it has been observed subsequently using taste aversion in rats (Taukulis & Revusky, 1975), magazine approach conditioning in rats (Pearce & Redhead, 1995), spatial learning in rats (Horne & Pearce, 2010), autoshaping in pigeons (Williams & McDevitt, 2002), and human causal learning (Aitken et al., 2000).

7 CS/US pre-exposure effects

In this section, we discuss benchmarks that arise from non-reinforced stimulus presentation prior to CS-US acquisition.

7.1 US pre-exposure effect (AA)

Presentation of the US in a training context prior to Pavlovian CS–US pairings retards the acquisition of the CR to the CS.

See Table S2.

Prior exposure to the US before initiating CS-US pairings retards the formation of an excitatory CR, a phenomenon known as the *US pre-exposure effect*. This effect has been demonstrated across various species and procedures (for a review, see Randich & LoLordo, 1979). In rats, it has been shown in conditioned suppression, conditioned ejaculatory preference, appetitive conditioning, conditioned taste aversion, and eyelid conditioning. The effect has also been observed in classical fear conditioning in honeybees, autoshaping in pigeons, eyeblink conditioning in rabbits, and evaluative conditioning in humans. The US pre-exposure effect has been observed in studies primarily investigating learned irrelevance, where a US pre-exposure group was included as part of the experimental design (e.g., Baker & Mackintosh, 1977).

A few studies did not demonstrate the US pre-exposure effect. For example, Armstrong (2019) reported an enhancement of oculomotor avoidance during CS-US

pairings following US pre-exposure in a Pavlovian disgust conditioning study, contrary to the expected response. Similar null findings have been reported in rats using drugs as the US. In such cases, pre-exposure to the drug may diminish its aversive properties during initial nicotine exposures, thereby facilitating the appetitive response to the CS.

Noncontingent reinforcer deliveries given before instrumental training have occasionally been reported to interfere with the acquisition of instrumental responding in rats (Dickinson, 1996; Lopez et al., 1992), although this effect does not appear to be universal (Beatty & Maki, 1979) and its boundary conditions have yet to be determined.

7.2 CS pre-exposure effect (latent inhibition) (A)

Pre-exposure to a CS followed by CS–US pairings retards the acquisition of the CR.

Domains: Fairly general in several species, but inconsistent or narrower in humans, pigeons, fish, and invertebrates

See Table S2.

The *latent inhibition* (LI) effect refers to retarded acquisition of responding to a CS that has previously been presented without the US (Lubow, 2010). The preexposure procedure is identical to that producing *habituation*, where habituation usually refers to reduced unconditioned responding to the preexposed CS, whereas LI refers to retarded acquisition of a CR during CS-US pairings.

LI was first observed in goats and sheep using a conditioned emotional response procedure, with a foreleg shock as the US, leg flexion as the CR, and either a flashing light or a turning rotor as the CS (Lubow & Moore, 1959). Since then, it has been documented across numerous species, including mammals (sheep, goats, rabbits, mice, rats, cats, dogs, monkeys, and humans), birds (pigeons), insects (honeybees, assassin bugs, fruit flies), crustaceans (crabs, crayfish), mollusks (snails), and amphibians (newly laid wood frog eggs). LI has been observed in various Pavlovian procedures, such as conditioned taste

aversion, conditioned suppression, eyelid blink and nictitating membrane conditioning, salivary conditioning, pinna reflex, leg flexion, orientation responses, and human contingency/predictive learning (for a review, see Lubow, 2010; and Table S2 for a detailed overview). There are also demonstrations in instrumental learning (Ackil & Mellgren, 1968).

Despite its broad applicability across species and procedures, LI sometimes requires special conditions (Lubow, 2010). In non-human animals, simple CS pre-exposure usually delays CR acquisition. However, in adult humans, simple pre-exposure rarely produces LI without a masking task during the pre-exposure stage (Byrom et al., 2018) with a few exceptions (Aranzubia-Olasolo et al., 2024). There is a suggestion that LI depends on the time interval between pre-exposure and conditioning (Best & Gemberling, 1977). Holland (2018) found CS-preexposure under select conditions could even facilitate subsequent acquisition of goal-directed CRs in rats (see also benchmark 7.4). Evidence for LI in invertebrates is limited by design and statistical issues, as habituation and sensitization can confound or mimic LI. Similarly, LI findings in pigeons are inconsistent depending on the procedure, and there is minimal evidence of LI in fish.

7.3 A change of context disrupts latent inhibition (A)

Domains: Domain-general in Pavlovian conditioning with partly unknown boundary conditions

See Table S2.

The deficit in acquisition of the CR produced by CS pre-exposure, termed *latent inhibition* (LI, see benchmark 7.1), is attenuated when pre-exposure and conditioning are conducted in two different contexts. Lubow (1976) reported this effect in rats (using odors as CSs and food pellets as US) and 5-year-old children (using geometric objects as CSs and marble-finding as the outcome). It has been demonstrated with both appetitive

(i.e., magazine approach, predictive learning) and aversive (i.e., conditioned suppression) in rats (e.g., Channell & Hall, 1983), snails (Muñiz-Moreno & Loy, 2022), pigeons (e.g., de la Casa & Ruiz, 1990), and adult humans (e.g., Zalstein-Orda & Lubow, 1995). LI attenuation has also been reported with changes in the time of day (morning vs. evening), and even when introducing a retention interval between pre-exposure and conditioning serves as a context change (see table S2 for a detailed overview).

The effect of LI attenuation due to a context change in conditioned taste aversion has been widely observed but has been found to have limitations. Using the time of day as context, LI attenuation occurs in an ABA design (pre-exposure, conditioning, and testing contexts), with variations observed across age groups (Manrique et al., 2009): increased LI in adolescent rats (post natal day [PN]48 and PN64), but reduced LI in adults (PN100). Physical context changes in preweanling rats (PN13) have also shown LI attenuation in a BAA design. These findings highlight the need for further research to clarify the boundaries of context-related effects on LI in conditioned taste aversion.

A study conducted by Nelson (2022) found that context change enhanced LI in humans, contrary to findings from at least ten prior studies, including some by the same authors. Using eye tracking, the study revealed that context change increased LI in goal trackers (focused on outcome locations) but attenuated LI in sign trackers (focused on the CS area). These results suggest individual differences exist in the context dependency of LI that are yet to be fully established.

7.4 Pre-exposure to a discriminant CS facilitates learning (perceptual learning) (A)

Exposure to similar stimuli, A and B, leads to faster subsequent acquisition of a discrimination between them.

Domains: Instrumental conditioning in rats and birds, conditioned taste aversion and appetitive Pavlovian conditioning in rats, evaluative conditioning and predictive learning

Learning about two CSs coupled with distinct outcomes (e.g., A-US, B-noUS) is facilitated by previous exposure to the CSs (Gibson & Walk, 1956). Behaviorally, this is observed by faster acquisition of the discrimination and/or a larger CR difference between the two CSs at test, or in other words, better discrimination of the CSs (for a review, see Mitchell & Hall, 2014). This phenomenon, often termed *perceptual learning*, has been demonstrated in various instrumental conditioning procedures including visual and auditory CSs in several infrahuman species including rats and birds (Mitchell & Hall, 2014), as well as in conditioned taste aversion and appetitive Pavlovian conditioning in rats (Artigas & Prados, 2017; Mitchell & Hall, 2014; Mondragón & Murphy, 2010). Studies in humans have largely been conducted in non-reinforcement settings (Mitchell & Hall, 2014); however there are several demonstrations of it using human evaluative conditioning and predictive learning tasks (Dwyer et al., 2004; Mundy et al., 2006, 2007, 2009; Nelson & Sanjuan, 2009).

Usually, the two CSs have common elements, or are at least in the same sensory modality, and several studies suggest that perceptual learning is not observed when there is no common element (e.g. Mackintosh et al., 1991). The effect is typically stronger when exposure to CS1 and CS2 is given in an intermixed fashion, as compared to separate blocks of exposure (Dwyer et al., 2004; Mundy et al., 2006, 2007, 2009; Nelson & Sanjuan, 2009).

Discussion

Looking back at more than 100 years of empirical research on associative learning, the body of evidence is massive, and the pace of discoveries is continuing. At the same time, theories struggle to explain even the full space of widely observed and highly generalizable empirical observations that have been known for over 50 years. The time it would take a single scholar, or a small group of scholars, to survey the vast and yearly

increasing literature constitutes a barrier to developing a comprehensive theory that integrates all findings. While reviews and meta-analyses appear regularly, they typically focus on an individual phenomenon or a small number of phenomena, and are frequently driven by theoretical considerations mandated by particular frameworks. One consequence of this is that theories typically seek to explain a small number of phenomena in what one might call an explanatory niche.

In the current work, we sought to stimulate the development of comprehensive theories by achieving two goals. First, we aimed at providing a comprehensive, structured, and iterative assessment of the empirical evidence, by grouping it into procedurally-defined categories of phenomena. While none of the phenomena are comprehensively reviewed here, we cited, where possible, either existing reviews or an appreciable number of examples for each phenomenon, which can serve as a basis for future systematic or meta-analytic efforts. Our second aim was to prioritize findings according to their levels of evidential credibility and thereby provide criteria on what to explain.

We believe that strong candidate theories should be able to explain robust and generalizable observations. Furthermore, as our field spans multiple species from invertebrates to humans, we believe that there must be theory development on many levels, including attention to phylogenetic differences and similarities. Species-general theories can provide accounts of learning that are relevant for all animals, even if the implementation details will differ between species. Species-specific theories can fill in detail and consider constraints of the respective environmental characteristics, ecological niches, and neural, perceptual, and behavioral systems. Finally, at least in mammal species that appear to possess partly separate neural systems to learn about appetitive and aversive events and predict and take actions to influence these events (Dayan & Berridge, 2014; LeDoux, 2000; LeDoux et al., 2017), domain-specific theories might emerge (but see

Heyes et al., 2020). Thus, different from the previously mentioned approach for working memory (Oberauer et al., 2018), species and task domain form important considerations in the present work.

We took several steps to maximize the breadth and depth of knowledge considered in this review. First, we recruited a diverse and representative panel of experts, many of whom work with multiple model organisms to investigate learning. Second, we solicited information concerning candidate phenomena from several different sources, including a survey of an additional 76 experts. While this survey yielded additional insights and led to the consideration of additional candidate phenomena, the majority of suggestions converged on the ones already included in a previous database, which collectively suggests that our efforts were successful. Grading was based on discussion and consensus across the entire author group, rather than only the topical experts, which meant that efforts were made to justify and explicate even niche phenomena to a broader audience. Finally, we consulted the expert community again on the gradings, which yielded largely consistent results.

Nonetheless, we cannot be fully sure that all possible candidates are included and that we did not overlook parts of the literature. This is why we provide an online forum for feedback, in particular, candidate phenomena and additional references supporting existing benchmarks (https://bachlab.github.io/associative_learning_benchmarks). Indeed, some phenomena, while informally observed in many laboratories, including among the authors, are rarely systematically reported. We speculate that the expert survey may have been more influenced by such informal observations, as well as by what one might call textbook knowledge, than the author group, and that this explains the (relatively sparse) discrepancies between our and the survey gradings. Such discrepancies, however, will hopefully spark new efforts for systematic characterization

of what might appear obvious to many research practitioners. We offer this list of rated benchmarks as being a fairly accurate reflection of current knowledge. As time passes, newly published data will call for this list, including the ratings, to be revised. Hence, we hope that future researchers see fit to update and publish successors to this list at regular intervals.

In relation to our first goal, we hope to have achieved a comprehensive overview of the field, providing insight concerning where research is most needed. Indeed, some phenomena commonly cited in textbooks and/or seen as critical tests of certain classes of theory – for example, the cue-to-consequence effect or external inhibition – received relatively low grades, typically due to limited or inconsistent empirical evidence. This might spark new research to conclusively demonstrate them (or not, as the case may be). On the other hand, there might be relatively little use in proving already well-known facts in slightly different settings. However, even a quick glance at our review will reveal that some research procedures are used a lot more often than others. The reasons for this might be rooted in research traditions and psychological motivations of the experimenters, such as the urge to flock with other researchers. But there might also be deeper scientific reasons why some effects are more readily demonstrated in one procedure than another. While not yet systematically investigated, this could become an important focus of future research.

Our second goal was to provide benchmarks for candidate theories, in particular, computational models of learning. While many models have been demonstrated to explain distinct sets of phenomena, the status of these phenomena has so far been unclear. Our work will simplify the interpretation of such simulations by prioritizing the evidence: a model that explains many AA benchmarks but fails on some C findings might have more explanatory value than one that explains many C benchmarks but contradicts AA

benchmarks. There is a bottleneck here in that simulations need to input information that captures experimental tasks and their parameters. While our work provides important leads, a quantitative survey of procedural parameters for the different benchmarks was far beyond the scope of a single benchmark review. Ultimately, however, the development of models would be greatly aided by a quantitative database of procedures, parameters, and expected results. We hope that this review might inspire such work in the future.

Finally, the benchmarks and their gradings should be seen as a snapshot of the evidence, not as a final verdict on the field. We have identified several instances where intuition, formed in many years of experimentation experience, contrasts with formal knowledge – for example regarding the influence of CS and procedural parameters on the pattern of CR. There are other instances where novel phenomena have not been investigated as much as yet, or where textbook findings were more recently called into question. Furthermore, new theories will inspire testing novel phenomena, which should be added to the list enclosed in this review. With our work, we hope to contribute to the continuing cycle of theory and experimentation.

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Supplementary results

In this section, we discuss all benchmarks graded B or C by the expert panel.

1 Acquisition

1.14 Conditioned diminution and facilitation of the unconditioned response (B)

After acquisition, the response to the US in a CS-US presentation is diminished or facilitated compared to the US not preceded by CS, depending on the setup and species.

Domains: Human aversive classical conditioning (diminution), rabbit eyeblink conditioning (facilitation)

See Table S2.

Following CS-US pairings, the unconditioned response (UR) to the US is attenuated (Kimble & Ost, 1961) or increased (facilitation) (Hupka et al., 1970) when the US is preceded by CS+, compared to the US (a) presented alone, (b) preceded by a CS-, (c) preceded by neutral stimulus, or (d) in an unpaired control group. A concept related to conditioned facilitation is Pavlovian sensitization (Domjan & Fanselow, 2024), whereby responding to a US or a non-US stimulus is increased in the presence of the CS. Here, we classify facilitated responding to non-US stimuli in the presence of a CS (such as fear-potentiated startle) as a type of CR, and focus on conditioned changes in responding to US. Note that the term *conditioned facilitation* has alternative meanings in the literature.

Conditioned diminution has been demonstrated almost exclusively in humans and in a single rat study (Fanselow & Bolles, 1979), as well as under specific circumstances in a single rabbit study (Donegan, 1981). In human aversive conditioning (including two reports of eyeblink conditioning), there are at least 12 reports, collectively including more than 500 participants, that show conditioned diminution across laboratories, protocol

variations, delay and trace conditioning, CS durations, CS types (visual and auditory), US types (electric shocks, loud sounds, corneal air puff, unpleasant picture and sound) and CR types (usually skin conductance responses but also eyeblink and cardiac responses). There is at least one report that UR diminution can be extinguished. Negative reports could not be identified.

Conditioned facilitation has been demonstrated consistently in rabbit eyeblink conditioning studies. There are at least 10 reports, collectively including more than 200 animals, that show conditioned facilitation across laboratories, protocol variations, delay and short-interval trace conditioning, CS durations, CS types (visual, auditory, vibrotactile), US types (periorbital shock, and corneal air puff) and conditioned response quantifications. One study reported that conditioned diminution occurs at stronger and facilitation at weaker periorbital shock amplitudes (Donegan, 1981). However, this has not been replicated, and other studies found facilitation across shock amplitudes (see Table S2 for a detailed overview). The same study suggested that rabbits' movement response to the periorbital shock is diminished when preceded by the CS, but this has not been replicated either. Finally, there is indirect evidence of conditioned facilitation in sexual conditioning (Domjan & Fanselow, 2024), and individual reports of this phenomenon in territorial intruder conditioning and food conditioning (Domjan & Fanselow, 2024).

1.15 Imperfect predictors effect (B)

An association CS-US2 is learned more rapidly after training CS-US1 with partial reinforcement rather than full reinforcement.

Domains: Domain-general in Pavlovian conditioning across non-human species with unknown boundary conditions

The acquisition of conditioned responding is sometimes faster for CSs that have been unreliable predictors of the same or other USs in the past, relative to CSs established as reliable predictors (Hall & Pearce, 1979, 1982). Evidence for the positive impact of uncertainty on new learning is robust in Pavlovian conditioning studies, where it has been supported by experiments conducted with appetitive and aversive conditioning across different species (Dickinson et al., 1976; Hall & Pearce, 1979, 1982; Haselgrove et al., 2010; Holland, 1984). This bias is possibly mediated by attentional processes, as measured by orienting reflexes (Wilson et al., 1992).

In humans, there is also strong evidence of enhanced attention to cues associated with uncertainty (Beesley et al., 2015; Chao et al., 2021; Hogarth et al., 2008; Ju & Cho, 2023; Le Pelley et al., 2016; Pearson et al., 2024) but whether or not this attentional advantage makes a difference in subsequent learning remains unclear. While some studies have found faster learning for cues associated with uncertainty under some conditions (Chao et al., 2021; Easdale et al., 2019) other studies have failed to detect any effect or found the opposite (for a review, see Le Pelley et al., 2016).

Note that this phenomenon is the opposite of the learned predictiveness effect (see benchmark 1.16), which has been investigated extensively in human contingency learning. At present, the conditions under which one effect or the other is observed remain poorly understood (for reviews of animal and human studies, see Pearce & Mackintosh, 2010; Le Pelley et al., 2016, respectively).

1.16 Learned predictiveness effect (B)

After training with compound CS such that one component A always predicts US1 while another component B is sometimes coupled with US1 and sometimes with US2, the association A-US3 will be more rapidly learned than B-US3.

Domains: Mainly human contingency learning, some non-human setups with unknown boundary conditions

Cues that have been established as good predictors of specific outcomes in the past show increased ability to become associated with new outcomes, relative to cues established as poorer predictors. The canonical demonstration of this effect, originally reported by LePelley and McLaren (2003a) and Lochmann and Wills (2003), has been replicated extensively in human predictive learning tasks (for a systematic review, see Le Pelley et al., 2016). There is substantial evidence that the learned predictiveness effect is driven by an attentional bias. For instance, eye-tracking measures show that participants pay more attention to cues that predict outcomes reliably (Le Pelley et al., 2011). Studies with EEG or behavioral measures of attention (e.g., dot-probe tasks or attentional blink) also support this conclusion (e.g. Le Pelley et al., 2013).

Although the experimental design used in these studies cannot be easily implemented in the conditioning procedures typically employed in animal research, some animal studies do approximate the original design with converging results (e.g. Dopson et al., 2010). Animal studies relying on alternative designs and procedures have also provided compelling evidence of faster learning with stimuli that have been previously established as good predictors (for reviews, see Le Pelley & McLaren, 2003b; Pearce & Mackintosh, 2010). This notwithstanding, some studies have yielded the opposite result: an advantage for previously imperfect predictors. At present, the conditions under which one effect or the other is observed remain poorly understood (Le Pelley et al., 2016; Pearce & Mackintosh, 2010); see also benchmark 1.15, “Imperfect predictors effect”.

1.17 More intense CSs facilitate acquisition (B)

When CSs are further away from a perceptual baseline (usually more intense), acquisition is faster or the CR asymptote is higher.

Domains: Aversive Pavlovian conditioning in several species (rats, rabbits, and humans)

In rats, this has been demonstrated for auditory CS loudness, auditory CS duration, and visual CS luminance, in a conditioned suppression procedure with foot shock US in both delayed and trace conditioning (Kamin, 1965; Kamin & Brimer, 1963; Kamin & Schaub, 1963). An effect of taste and concentration was found in conditioned taste aversion (Dragoin, 1971). In rabbits and humans, an effect of auditory CS loudness was found in eyeblink conditioning (Beck, 1963; Grice & Hunter, 1964; Scavio & Gormezano, 1974). One study demonstrated that learning rate increased when CS loudness was further away, either above or below, background stimulus loudness in rats (Kamin, 1965). Of note, the phenomenon has been tested with a limited range of intensities, and the effect presumably becomes smaller as the base intensity increases.

No further replications could be identified. Much of the later conditioning literature has absorbed the propensity of a CS to induce conditioning into the concept of a CS-specific learning rate, which is inferred from data rather than assumed a priori. Effects of CS intensity on other benchmarks (e.g., latent inhibition, blocking, overshadowing) are discussed within the respective benchmarks.

1.18 Backward conditioning elicits CRs (B)

Domains: Mainly rat conditioned suppression, occasionally other preparations in rats, rabbit eyeblink conditioning, human autonomic conditioning

Backward conditioning is a procedure in which the CS onset is after the US onset, and the CS often also continues after US offset. Thus, the CS is not temporally predictive of the US. A related procedure often studied in parallel is simultaneous conditioning, where CS and US onsets coincide.

In rats, presentation of the CS after aversive backwards conditioning generally leads to a suppression of instrumentally conditioned lever pressing or licking (collectively termed conditioned suppression), as shown in several studies across laboratories and procedural variations (Bevins & Ayres, 1992; R. Chang et al., 2004; R. C. Chang et al., 2003; Cole & Miller, 1999; Dolan et al., 1985; Heith & Rescorla, 1973; Heth, 1976; Williams et al., 1986). There are individual reports of backwards-conditioned avoidance (Keith-Lucas & Guttman, 1975), backwards-conditioned punishment (Williams et al., 1986) and backwards-conditioned reinforcement (Urushihara, 2004), as well as of backwards-conditioned magazine approach (Navarro et al., 2023), backwards-conditioned eyeblink CR in rabbits (Wagner & Terry, 1975), and backwards-conditioned autonomic responses in humans (Homzie et al., 1964; Zeiner & Grings, 1968). In rats, backwards-conditioned suppression occurs even after one conditioning trial (Bevins & Ayres, 1992) and appears to diminish with the number of conditioning trials (Cole & Miller, 1999; Heth, 1976). When the US was already predicted in time by a different CS, neither conditioned suppression (Dolan et al., 1985) nor eyeblink conditioning (Wagner & Terry, 1975) occurred.

In indirect tests, however, backwards-conditioned CS might exhibit inhibitory properties, for example delaying acquisition of another association of the same valence (Siegel & Domjan, 1971) or conditioned inhibition in summation tests (Barnet & Miller, 1996). It has been suggested that when coupled with a second-order CS, the CR depends on the predicted temporal relation of the second-order CS and US (Arcediano et al., 2005; Barnet & Miller, 1996). There are also reports that for prolonged CSs, conditioned excitation is more apt to occur with shorter ISIs and conditioned inhibition with longer ISIs (Romaniuk & Williams, 2000). Finally, it has been suggested that backwards conditioning is underreported (Spetch et al., 1981).

1.19 Acquisition is context-dependent (B)

A CR is stronger when tested in the same context as opposed to a different context from acquisition.

Domains: Human predictive learning, Pavlovian conditioning in rats

Conditioned responding often becomes context-dependent for ambiguous stimuli that have been paired with conflicting outcomes (e.g., extinction or counterconditioning following acquisition). There is evidence that, under certain circumstances, this can also happen for stimuli that have only been paired with one outcome and, therefore, are not ambiguous.

A partial loss of conditioned response with a change in context has been reported in taste aversion by rats (Sjödén & Archer, 1989), conditioned fear (Hall & Honey, 1990), classical appetitive conditioning (Bouton & Sunsay, 2001), and human predictive learning (Ogallar et al., 2019). However, the sparsity of context-switch effects with unambiguous information, despite an extensive literature on the renewal effect (Bouton, 1993), suggests that this effect depends on specific boundary conditions that determine whether and when unambiguous information becomes context-dependent or not.

First, responding to a cue has been found to be context-dependent early in training but not when training is extended or when the organism receives extensive exposure to the experimental contexts (León et al., 2011; C. E. Myers & Gluck, 1994). Second, responding to a cue can become context-dependent if the acquisition is conducted concurrently with the extinction of a non-target cue (Rosas & Callejas-Aguilera, 2006) or after the extinction of a non-target cue (Bernal-Gamboa et al., 2013). Third, responding to a cue has been shown to become context-dependent when acquisition takes place while another cue is being trained under partial reinforcement (Abad et al., 2009; Bouton & Sunsay, 2001). Fourth, context-specificity of an unambiguous cue has been found in both

human and nonhuman animals when the cue is trained within contexts that become informative through conditional discrimination in which the meaning of non-target cues is reversed across contexts (Preston et al., 1986). Finally, Callejas-Aguilera and Rosas (2010a) found that unambiguous information becomes context-dependent when trained in the context in which both members of a different pair of cues are reinforced in half of the trials (pseudo-discrimination), disappearing when the pseudo-discrimination is changed to a true discrimination. Similar results have been found with other manipulations that are assumed to enhance subjects' attention to the context, such as providing instructions or increasing the salience of contextual cues (for a review, see Ogallar et al., 2017).

Context-dependency of responding to unambiguous cues has been extensively demonstrated in human predictive learning procedures (Rosas & Nelson, 2019), but some studies have not replicated these results (Nelson et al., 2011; Nelson & Lamoureux, 2015) suggesting that boundary conditions of the effect are not fully understood.

1.20 Cue-to-consequence effect (B)

Some combinations of CS and US elicit stronger CR than others.

Domains: Pavlovian conditioning, mainly involving nausea US in rats

CSs and USs interact to determine the CR, a phenomenon termed the *cue-to-consequence effect* (Garcia & Koelling, 1966). Garcia and Koelling (1966) exposed rats to a flavor and an audiovisual cue. If these CSs were followed by a poison US, rats avoided only the taste CS, whereas if they were followed by a foot shock US, they avoided only the audiovisual CS. This has been replicated in different laboratories (Domjan & Wilson, 1972; Garcia et al., 1968; Green et al., 1974). The strong conclusion of the initial work, that is, that rats cannot learn the association of an audiovisual CS and nausea US, has been refuted since (Dwyer et al., 2017; Gasalla et al., 2017; López et al., 2019). However, the weaker

assertion that CRs are modulated by an interaction of CS and US is well-supported by additional evidence. For example, an interaction has been reported between auditory vs. visual CSs on the one hand, and aversive vs. appetitive USs in pigeons (Foree & LoLordo, 1973), and foot shock vs. nausea USs in rats (V. Miller & Domjan, 1981), respectively. Thus, the cue-to-consequence effect appears to reflect quantitative rather than qualitative differences.

This phenomenon is graded B based on a small number of studies in a limited number of rather specific procedures and the presence of many counterexamples. Nonetheless, the effect is well-known and presented in many introductory textbooks, which might explain the median rating of AA the phenomenon received in the expert survey.

1.21 Benefit of retrieval practice (B)

Repeated retrievals increase the CR.

Domains: Mainly human predictive learning, rat spatial (instrumental) learning

The *retrieval practice effect* refers to the more general phenomenon whereby increased recall on a critical test is observed if, in the interval following a learning episode, a practice test is taken. The effect is also labelled the *testing effect* or *test-potentiated learning*. An associative learning example would involve initial learning of A-US, followed by a practice test (A-?) preceding the final recall test (A-?). Typically, practice tests enhance final recall compared to control groups that either do not take the practice test or are given a restudy opportunity (A-US) instead of the practice test. Benefits of retrieval practice are obtained even if no feedback is provided in the practice test. This may have implications for understanding the initial learning and storage mechanisms.

Meta-analyses and pre-registered experiments (e.g., Heitmann et al., 2021) have confirmed the robustness of the testing effect and also explored some of its boundary

conditions and moderators (Rowland, 2014; Yang et al., 2021). Non-human research, however, is very sparse. Some studies have used reminder treatments, equivalent to tests, to aid memory recovery in animal models of amnesia. Polack and Miller (2022) review this and a small number of related phenomena that can plausibly be construed as animal equivalents of testing effects (see R. R. Miller, 1982 for an example of it in spatial learning by rats).

1.22 Partial reinforcement acquisition effect (PRAE) (C)

Acquisition is slower or the CR asymptote is lower during partial rather than continuous reinforcement.

Domains: Pavlovian conditioning across species, with a substantial proportion of negative and some opposing reports

See Table S2.

The partial reinforcement acquisition effect (PRAE) is typically tested by comparing two groups that receive the same number of US in different reinforcement schedules (Gonzalez et al., 1962). The phenomenon is often reported as a secondary finding in studies investigating the partial reinforcement extinction effect (PREE, see benchmark 4.6).

PRAE has been observed in different laboratories, various species (fish, pigeons, rats, rabbits, and humans), aversive and appetitive domains, and for different CRs (general activity, CS approach, eyeblink conditioning, jaw movement, and CS consumption in taste conditioning), see table S2 for a detailed overview. While we are not aware of a systematic review or meta-analysis in the past 20 years, we identified a large proportion of studies reporting no difference between fully reinforced and partially reinforced groups, calling into question the phenomenon's robustness. More rarely, the opposite effect is also observed. Various boundary conditions have been discussed, but most of

them have not been experimentally confirmed. Some reports suggest that the cumulative time of non-reinforced CS presentation, rather than the reinforcement rate per se, determines the strength of the CR (Chan & Harris, 2017).

This phenomenon is graded C based on lack of robustness, as evidenced by a large proportion of null or even opposite findings. Nonetheless, the effect is presented in many introductory textbooks, which might explain the median rating of A that the phenomenon received in the expert survey.

1.23 CS-specific CR (C)

The pattern of the CR depends on the CS.

Domains: Specific appetitive and aversive conditioning procedures in rats.

The pattern of the CR can depend on the CS employed in a conditioning procedure. Holland (1977, 1979) observed and quantified a number of different rat behaviors in response to light and tone CSs (e.g., rear, perambulate, head jerk) and found differential patterns to these two CS, especially during the early part of the CS. To our knowledge, there are no published replications of this work from other laboratories.

Furthermore, it is often found that the magnitude of an individual CR depends on the nature of the CS. For example, rats show a greater CR when the CS is auditory rather than visual. In itself, this does not speak to the nature of the CR; the animal could simply be learning more or less, due to limitations of their sensory systems. Some work, however, has reported CRs of different magnitude to visual and auditory CS, but at the same time equal responding on indirect learning metrics (blocking, second-order conditioning, overexpectation, conditioned suppression) (Bevins & Ayres, 1991; Kim et al., 1996). This would suggest that learning is the same for visual and auditory CS, but that the type of CS influences how that learning is expressed in behavior. Both studies came from the same

laboratory, and none of the specific tests reported have been directly replicated within or across laboratories.

This phenomenon is graded C based on lack of systematic published investigation; however, according to our collective experience with various learning procedures, it is likely to be more robust. We suggest that such informal or unpublished observations might explain the median rating of AA that the phenomenon received in the expert survey.

1.24 Parameter-specific CR (C)

The pattern of a CR depends on the parameters of the conditioning schedule.

Domains: Systematically studied in several relatively narrow Pavlovian conditioning procedures.

The pattern of the CR can depend on parameters of the conditioning procedure, when CS and US are kept constant. While informal observations of this phenomenon abound, systematic investigations are quite scarce. One potential reason is that researchers typically seek to adjust the conditioning procedure in order to maximize one specific CR, which is then used as singular or primary endpoint of investigations. As one conditioning parameter, variation of ITI has been relatively systematically examined. In rat reward conditioning as well as in one quail sexual conditioning study, longer ITIs shift the balance of CS approach (often called *sign-tracking*) and US approach (often termed *goal-tracking*) in favor of CS approach (Burns & Domjan, 2001; Lee et al., 2018; Mahmoudi et al., 2023; Thomas & Papini, 2020).

Although less well investigated, partial reinforcement also appears to shift the balance towards CS approach over US approach compared to continuous reinforcement (Davey & Cleland, 1982). In addition, there are two older reports that shorter ISIs favor the display of nictitating membrane responses over heart rate changes after eyeblink conditioning with rabbits (Meredith & Schneiderman, 1967; Vandercar & Schneiderman,

1967). In humans, skin conductance and pupil size responses might dissociate as a function of the number of acquisition trials in autonomic conditioning, but we could identify only one systematic investigation (Tzovara et al., 2018).

This phenomenon is graded C based on lack of systematic investigation; however, according to our experience with various learning procedures, it is likely to be more robust. We suggest that such informal or unpublished observations might explain the median rating of A that the phenomenon received in the expert survey.

1.25 Inverse base-rate effect (C)

When a compound cue AB is paired with US1 more frequently than compound cue AC is with US2, the novel compound cue BC elicits the CR associated with US2.

Domains: Human predictive learning

Human judgments and choices often incorporate base-rate information in a directionally-normative way, but the inverse base-rate effect (IBRE; Medin & Edelson, 1988) is an example of counter-normative behavior. In the standard design, participants observe a compound cue (AB) associated with US1 and another compound (AC) associated with a different US2. Cue A is common to both compounds, and AB-US1 trials are more frequent than AC-US2 trials (typically by the ratio 3:1). The IBRE refers to the observation that human participants tend to predict US2 when tested with the novel compound BC. This is striking, as one component of BC, namely cue B, has been paired more often with US1 than the other component, C, has been with US2.

The IBRE is a robust phenomenon replicated in a substantial number of studies (see Don et al., 2021 for a detailed literature review), albeit largely specific to human predictive learning. It represents a significant challenge to many theories of associative learning. Non-human research is very sparse: Don et al. (2021) mention one relevant study with baboons.

2 Generalization

2.5 External inhibition (C)

Adding a novel cue B to a trained cue A results in less responding than the trained A by itself.

Domains: Widely observed in Pavlovian and instrumental conditioning but often as an incidental finding without statistical tests, and there are a considerable number of null results with unknown boundary conditions

External inhibition was first reported by Pavlov (1927), who noted that the same stimulus that produced external inhibition also produced the opposite effect, disinhibition (increased CR after extinction of A). The effect has later been reported by Wenger (1936) in human autonomic conditioning, with rats in a runway procedure (Gagné, 1941) and in rabbit eyeblink conditioning (Brandon et al., 2000). Thorwart and Lachnit (2009a, 2010a) found the effect in multiple experiments in human predictive learning using configurations of dots on screen as stimuli, and also in a causal learning task (Experiment 2, Thorwart & Lachnit, 2010b). Note however, that many of these demonstrations are reported as incidental findings and are not accompanied by statistical tests.

There are several null findings. Glautier (2004) did not observe the effect in a human predictive learning task, and Wheeler et al. (2006) found a non-significant effect in two experiments with human predictive learning. Kehoe (1994, experiments 2-3) did not observe the effect when the added stimulus was in the same modality as the trained stimulus, and even observed the opposite result in Experiment 3 in which the added stimulus was from a different modality. González (2003) also did not observe the effect in two experiments with fear conditioning in rats. It is not clear whether the null effects can be explained by the modality of the added stimulus (Soto et al., 2014) or some other factor.

Our C grading partly reflects the fact that the phenomenon is often reported incidentally without statistical tests. However, the frequency of these observations might suggest that it is in fact more robust, which might explain the AA median grading that it received in the survey.

3 Discriminations

3.13 Interference by a common cue in negative patterning (B)

When training with intermixed presentations of two individual stimuli followed by a US (A+, B+) and a compound of those two stimuli followed by no US (AB-), the discrimination is acquired slower when a common stimulus is added to all trials (AX+ / BX+ / ABX-).

Domains: Pavlovian and instrumental conditioning in rats, pigeons, bees, humans, usually using within-modality stimuli; but opposing findings with unclear boundary conditions

Typically, the addition of the common cue results in retardation and also in a reduced difference in responding between the reinforced and non-reinforced trial types. This interfering effect of adding a common cue has been replicated in several species, including rats (Rescorla, 1972), pigeons (Pearce & Redhead, 1993), bees (Chandra & Smith, 1998) and humans (Redhead & Curtis, 2013), using both Pavlovian and instrumental procedures. In most cases, this has been observed using within-modality stimuli. For instance, Pearce and Redhead (1993) compared negative patterning discriminations with (versus without) the added common cue in a pigeon autoshaping procedure. The stimuli were distributed dots of different colors displayed on a computer screen. Acquisition of the discrimination was worse in the presence of the common cue.

In other procedures, the effect of adding the common cue is less clear. Some experiments have found that the addition of the common cue causes improved

discrimination, possibly suggesting that the modality and/or similarity of the stimuli may be important (see e.g. K. M. Myers et al., 2001). Consistent with this suggestion, Redhead and Curtis (2013) found evidence, in human causal learning, that the addition of the common cue could facilitate or retard acquisition of negative patterning depending on the modality of the predictive stimuli.

There are related effects observed with other complex versions of negative patterning discrimination, some of which also show sensitivity to stimulus properties. For instance, given a discrimination between A+ / BC+ / ABC-, discrimination between BC and ABC appears to be poorer than discrimination between A and ABC. This result has been found using within-modality stimuli in rats (Pearce, 1994) and honeybees (Chandra & Smith, 1998), though at least one study in human causal learning did not find this difference (Lachnit et al., 2008). Some evidence from human conditioning procedures suggests that the amount of time available to process the stimuli may be critical (Lachnit et al., 2013).

3.14 Biconditional discriminations are harder than negative patterning (B)

Discriminative responding between the US-present and US-absent trials of a biconditional discrimination (AB+ / BC- / CD+ / AD-) is more difficult than a discrimination between the US-present and US-absent trials of a negative patterning discrimination (A+ / B+ / AB-).

Domains: Rats appetitive Pavlovian conditioning and human causal learning, boundary conditions include the presence of a common cue and the CS duration

Human causal learning studies have demonstrated that biconditional discriminations are learned more slowly than negative patterning (Don et al., 2020; Harris & Livesey, 2008). There are relatively few direct comparisons of biconditional and negative patterning in other species; however Harris (2008) and Delamater (2017) found

that rats acquired a biconditional discrimination less effectively than they acquired negative patterning. In both of these studies, there was an initial period in which performance on the biconditional discrimination appeared to be better because the compound in the negative patterning discrimination elicited stronger responding than the reinforced single stimulus presentations. However, with more extended training, acquisition of the negative patterning discrimination became much stronger than the level achieved for the biconditional discrimination.

Some noteworthy opposing findings have been reported with variants of typical negative patterning and biconditional discriminations. For instance, Whitlow (2013) found, in human causal learning, that a negative patterning discrimination with an added and explicitly non-reinforced redundant cue ($X- / AX+ / BX+ / ABX-$) was acquired more slowly than a standard biconditional discrimination. Using causal learning, Whitlow and Loatman (2015) compared the learning of a biconditional discrimination to a negative patterning discrimination in which the single stimuli were paired with a different novel stimulus every time they were presented (e.g., $An+ / Bn+ / AB-$, where n was a novel stimulus). Under these circumstances, negative patterning was acquired more slowly than a biconditional discrimination. Delamater (2017) found that when two distinctive reinforcers (pellets and sucrose) were used as the two reinforced compounds of the biconditional discrimination and were combined with long CS durations, rats learned a biconditional discrimination more effectively than negative patterning.

3.15 Intra/extradimensional shift effects (B)

After discrimination training with CSs that differ on two perceptual dimensions, one CS predicting the US and another not, a subsequent discrimination with different CSs is facilitated if the previously predictive dimension continues to be predictive and the other one not, rather than the other way around.

Domains: Many species but only demonstrated in narrow experimental procedures mainly involving instrumental learning or pigeon autoshaping

Intradimensional/extradimensional (ID/ED) shift procedures involve training of two discrimination problems in successive order. The stimuli of the discrimination problems vary on two dimensions, and the particular values of the dimensions are changed from the first to the second discrimination ("total change design"; Slamecka, 1968). Each discrimination problem can be solved using the values of one dimension, while the values of the other dimension are irrelevant for the solution of the discrimination. The ID/ED shift effect refers to the observation that the second discrimination is acquired more rapidly when its relevant dimension had also been relevant for the first discrimination (and thus the other dimension was irrelevant for both discriminations), than when the relevant dimension on the second discrimination had been irrelevant on the first (and thus the irrelevant dimension on the second discrimination had been relevant on the first). The ID/ED shift effect has been primarily shown for various forms of instrumental conditioning tasks in humans (Eimas, 1966), non-human primates (e.g., Roberts et al., 1988), pigeons (Mackintosh & Little, 1969), rats (Birrell & Brown, 2000), and honey bees (e.g., Klosterhalfen et al., 1978). More rarely, it has also been demonstrated for Pavlovian conditioning using autoshaping in pigeons (George & Pearce, 1999).

3.16 Transfer along a continuum (easy-to-hard effect) (B)

Discrimination training with two CSs that are highly discriminable facilitates subsequent discrimination training with CSs that are more similar to each other.

Domains: Instrumental conditioning across species, eyeblink conditioning in rabbits; contradictory results in conditioned taste aversion and unclear boundary conditions.

Learning about two CS coupled with distinct outcomes (e.g., CS1-US, CS2-noUS) is facilitated by previous training with a set of two different CSs that are easier to distinguish on the same dimension (Lawrence, 1952). Behaviorally, this is observed by a larger CR difference between the two CS at test, or in other words, better discrimination of the CS (for a review, see Hall, 1991). This phenomenon has been demonstrated in various instrumental conditioning procedures across species, as well as in conditioned taste aversion in rats (Arriola et al., 2014, 2015), but see Scahill and Mackintosh (2004) for a conflicting finding, and one in rabbit eyeblink conditioning (Haberlandt, 1971).

3.17 Feature-positive discriminations are easier than feature-negative discriminations (C)

Given a discrimination in which the compound of two stimuli (AX) leads to a different outcome than one of the stimuli presented individually (X), discriminative responding develops faster when the compound predicts the US (feature positive) than when the compound predicts the absence of the US (feature negative).

Domains: Mainly rat conditioned suppression, pigeon and human instrumental conditioning; unclear boundary conditions, and opposing results in humans.

Discriminations are often easier to learn if the presence of a feature A predicts the US (feature-positive discrimination, AX+/X-) rather than its absence (feature-negative discrimination, X+/AX-). This is often termed the *feature positive effect* (FPE) and is usually demonstrated in a between-subjects design in which one group receives feature-negative and another receives feature-positive training. The FPE was first reported by Jenkins & Sainsbury (1969) in pigeon instrumental learning, replicated for example, by Hearst (1988), and was also shown in Pavlovian conditioning in rats with foot shock US and conditioned suppression as CR (Reberg & Leclerc, 1977), as well as instrumental learning in humans with key presses as CR and “task points” as US (Lotz, et al., 2012;

Newman et al., 1980; Richardson et al., 1987). In pigeon instrumental learning, the FPE has also been found when the positive feature did not unambiguously signal the US and was intermittently presented alone during the ITI (Hearst, 1988). In human instrumental conditioning, the FPE has occasionally been reported in within-subjects designs (Richardson, & Massel, 1982). However, there are some contradictory results in human instrumental conditioning, where a pronounced feature-negative advantage across different experiments has been reported, with unclear boundary conditions (Fiedler et al., 1989).

Our C grading is based on the small number of studies directly contrasting feature-positive and feature-negative discrimination, a limited range of procedures, and opposing results seen with humans. It is possible that more published or unpublished (potentially informal) replications of this phenomenon in other domains exist, which might explain the A median grading in the survey.

3.18 Feature ambiguous occasion setting (C)

In serial discriminations, one stimulus (X) can be trained to concurrently serve as the feature in both a feature-negative discrimination ($A+ / X \rightarrow A-$) and a feature-positive discrimination ($B- / X \rightarrow B+$) when combined with different stimuli (A / B).

Domains: Rat appetitive (Pavlovian and instrumental) conditioning, only few demonstrations

Feature-ambiguous occasion setting is demonstrated in a scenario where a feature (A) indicates both that one target will be followed by reinforcement ($X-; AX+$) and that another target will not ($Y+; AY-$). The phenomenon refers to the observation that animals can use the feature to solve the discrimination. In these scenarios, the relationship between the feature and reinforcement is ambiguous. Thus, the feature alone conveys no relevant information regarding future reinforcement. This suggests that the feature's

ability to act in feature-positive and feature-negative discriminations is independent of other processes and immune to summation.

Feature-ambiguous occasion setting has not been investigated as frequently as other discriminations. This is likely due to the preparation having many similarities to a simple biconditional discrimination (AX+, AY-; BX-, BY+) but it is typically assessed with a single feature whose presence or absence *alone* serves to disambiguate the target stimuli (i.e., in the biconditional discrimination B could be thought of as NOT A). The strongest evidence arises from two experiments from Holland's laboratory where rats acquired a feature-ambiguous discrimination (X-, AX+; Y+; AY-) where a light served as the feature and two separate auditory stimuli served as the targets X and Y (Holland, 1991; Holland & Reeve, 1991). It should be noted that almost all evidence makes use of serial preparations where a trace interval is introduced between the feature and target. The rate of acquisition was comparable to animals trained on separate feature-positive and feature-negative discriminations. Intriguingly, separately trained features only transfer within the domain; that is, a feature B that served separately as a feature-positive occasion setter only transferred to increase responding to X but did not reduce responding to Y (Holland, 1991). Recently, a similar effect was demonstrated in Pavlovian approach learning in rats, where context served as feature (Peterson et al., 2023).

4 Extinction

4.9 Reinstatement (B)

After extinction, presentation of the US in the same context partially restores responding.

Domains: Domain-general across species with a proportion of weak results and partly unknown boundary conditions

First reported by Pavlov (1927) in a conditioned salivation procedure in dogs, the reinstatement effect has been investigated most extensively in rodents with Pavlovian and instrumental procedures (e.g., Rescorla & Heth, 1975; Bouton & Bolles, 1979; Rescorla & Cunningham, 1977; Bouton, 1984; Bouton & King, 1983; A. G. Baker et al., 1991), mainly in the context of assessing the learning mechanisms engaged during extinction. The first demonstrations in humans emerged only decades later (e.g. Dirikx et al., 2004, 2007, 2009; Hermans et al., 2005; LaBar & Phelps, 2005; Norrholm et al., 2006; Schiller et al., 2008). The work in humans and a brief historical background of rodents studies were reviewed by Haaker et al. (2014a). In addition to demonstrations in humans and other vertebrates, reinstatement has also been demonstrated in invertebrates, including crabs (Hepp et al., 2010), crayfish (Nathaniel et al., 2009), honeybees (Plath et al., 2012), and snails (Alvarez et al., 2014).

The reinstatement effect has been shown to be largely context-dependent in rodents (Bouton & Bolles, 1979; Bouton & King, 1983; R. F. Westbrook et al., 2002) and humans (Sjouwerman & Lonsdorf, 2019, 2023). In rodents, a role of context conditioning in the reinstatement effect has been demonstrated (Bouton & King, 1983, exp. 3), and the effects were shown to be specific to the extinguished CS; CRs to unextinguished CS were not further enhanced (Bouton & King, 1986). Even though work in humans on the context dependency of the reinstatement effect is sparse (e.g., Sjouwerman & Lonsdorf, 2023), the overall pattern observed mirrors results from rodent work, despite procedural variations (e.g., single cue vs. differential conditioning) and different outcome measures used across species. There are reports suggesting that reinstatement effect is absent when the reinstatement US is different from the acquisition US in both rodents (Rescorla & Heth, 1975) and humans (Sokol & Lovibond, 2012), but see (García-Gutiérrez & Rosas, 2003).

In rodents, reinstatement effects have sometimes been demonstrated to enhance responding beyond renewal effects (R. F. Westbrook et al., 2002, exp. 3). In humans, reinstatement effects can often not be fully differentiated from non-associative processes or other recovery phenomena such as renewal (Haaker et al., 2014b; Lonsdorf & Sjouwerman, 2021), as contextual changes that are inherent to reinstatement manipulations may induce renewal effects that may obscure the observation of genuine reinstatement effects (Sjouwerman & Lonsdorf, 2023). In addition, in some human work, US exposure following extinction of a CS+ can cause responding to cues never paired with that US, for example, evidence of non-selective effects on responding to a CS- (for a review and discussion, see Haaker et al., 2014b). The boundary conditions for, and mechanisms of, such a generalized effect remain elusive.

4.10 Rapid reacquisition (B)

After CS-US acquisition and CS-noUS extinction, further CS-US presentations result in re-acquisition of the CR in fewer trials than during initial acquisition.

Domains: Across species and domains, but not in all procedures and with unclear boundary conditions.

Initially hinted at in the work of Pavlov (1927), rapid reacquisition can be observed in aversive and appetitive procedures alike (Napier et al., 1992; Ricker & Bouton, 1996). Whereas most demonstrations have focused on classical conditioning preparations, it also occurs in instrumental conditioning (Bouton et al., 2012). The phenomenon has also been established in humans (Kindt & Soeter, 2013; Lipp et al., 2021).

While the phenomenon is robustly demonstrated across a variety of preparations, it appears not to be universal. For instance, it is not readily demonstrated in conditioned suppression (Bouton et al., 2012) or flavor aversion learning (Hart et al., 1995) in rats. Moreover, some evidence indicates that even in preparations in which rapid reacquisition

occurs, it can be reduced by occasionally interspersing reinforced trials or unsignalled USs during extinction in rats (Bouton et al., 2004) and humans (Lipp et al., 2021; Morís et al., 2017). Also, the phenomenon can be prevented (Weidemann & Kehoe, 2003) through massive extinction training, or even reversed (Leung et al., 2007), so that reacquisition occurs at a slower pace than initial acquisition in rats.

Our B grading is based on the limited number of procedures in which this has been observed, and on unknown boundary conditions. We note that the similar concept of memory savings is widely observed in declarative memory research, which might have contributed to the AA median grading that the phenomenon received in the survey.

4.11 Recovery from counterconditioning (B)

After counterconditioning, the initial CR is partially recovered by the passage of time (spontaneous recovery), unsignalled US presentations (reinstatement), or change of context (renewal).

Domains: across Pavlovian conditioning domains in humans; limited evidence from other species or instrumental conditioning

See Table S2.

Recovery from counterconditioning (ReCC) refers to the phenomenon that conditioned responding (CR), diminished through counterconditioning (CC, see benchmark 4.2), is recovered as a result of manipulations of US reinstatement (see benchmark 4.9), context renewal (see benchmarks 4.3, 4.4, 4.17), or spontaneous recovery (see benchmark 4.8) (Brooks et al., 1995; Holmes et al., 2016; Keller et al., 2023). See Keller et al. (2020) for an authoritative and systematic review of ReCC, and see the respective benchmarks for a description of the experimental designs.

In humans, ReCC has been reliably demonstrated through spontaneous recovery, reinstatement, and ABA renewal with CSs including neutral human faces, fear-relevant

images, and neutral house pictures, with aversive USs including aversive sounds, electric shock, mutilated body pictures, with appetitive USs including positive sounds, positive images, funny film clips, with CRs including US1 expectancy ratings, CS valence ratings, skin conductance responses, and procedures including Pavlovian aversive-to-appetitive and appetitive-to-aversive conditioning, and thought conditioning (Kang et al., 2018; Keller et al., 2023; Quintero et al., 2024; van Dis et al., 2019; Van Gucht et al., 2013; Zenses et al., 2023). No ReCC was observed for subjective evaluative CR (fear of CS-related pain) when examining the reinstatement effect using an instrumental aversive-to-appetitive conditioning procedure (Gatzounis et al., 2022). Additionally, evidence regarding AAB and ABC renewal (compared to ABA renewal) is relatively sparse and mixed. Keller et al. (2023) found no AAB renewal for either subjective evaluative CRs (CS allergy rating) or behavioral CR (forced binary choice). They did find ABC renewal, but only for behavioral CRs (forced binary choice) (Keller et al., 2023).

In rats, one study by Brooks (1995) found ReCC for a behavioral CR (magazine entries) using reinstatement. This study found no reinstatement if the reinstatement manipulation was conducted in a context different from the acquisition context. While some previous studies included both CC and extinction groups and compared their CRs during the recovery phase, the absence of a direct comparison between the extinction/counterconditioning and recovery phases makes it challenging to assess the evidence for ReCC from these studies (Bouton & Peck, 1992; Correa et al., 2023; Holmes et al., 2016; Thomas et al., 2012).

Our B grading is based on the fact that this has been rarely observed outside human research. Here, however, it is relatively robust, which might have contributed to the AA grading it received in the survey.

4.12 Attenuation of renewal by multiple context extinction (B)

Conducting extinction in multiple contexts, rather than a single context, reduces the CR when testing occurs in the original acquisition context or an entirely novel context.

Domains: Rat and human fear conditioning.

In analogy to the corresponding standard renewal effects (see benchmarks 4.3, 4.4), we term the procedure ABA renewal when testing occurs in original acquisition context and ABC renewal when testing is in a novel context. The effect was first demonstrated by Gunther et al. (1998) in a conditioned suppression preparation in rats with ABC renewal, and was later demonstrated in humans (Balooch et al., 2012; Balooch & Neumann, 2011; Bustamante et al., 2016a; Glautier et al., 2013). However, the effect has not always been replicated in ABA- and ABC-renewal in rats (Bouton et al., 2006) nor in ABA-renewal in humans (Bustamante et al., 2016b). For a meta-analytic review, see Bustamante (2024).

The initial study (Gunther et al., 1998) moreover demonstrated that the attenuating effect of multiple-context extinction on renewal disappeared when initial conditioning was also conducted in multiple contexts.

4.13 Attenuation of renewal by retrieval cues (B)

After interspersing a specific stimulus during extinction training, the presence of this stimulus reduces the CR when tested in the original acquisition context or in an entirely novel context.

Domains: Rat magazine approach conditioning, human fear conditioning, only few observations but with no opposing results

In this procedure, the interspersed stimulus X is usually scheduled to appear before the first CS extinction trial and later during intertrial intervals, and then presented in the test context before the first CS test trial. The phenomenon was first observed by

Brooks and Bouton (1994) and the stimulus was coined *retrieval cue*, based on the assumption that this stimulus becomes associated with the extinction context and weakens CR renewal by retrieving the memory representation of the extinction context, which in turn retrieves a CS—noUS association. Only few studies have further investigated this phenomenon in human fear conditioning (Dibbets et al., 2008; Dibbets & Maes, 2011; Vansteenwegen et al., 2006).

A further difficulty is that many control conditions need to be in place to demonstrate that the effect of stimulus X at test is selectively due to its prior presentation during extinction. It is also unclear what the proper control is for presenting X during the renewal test. One possibility is to include a condition where X is presented during conditioning rather than extinction, and compare the effect of X on CR during renewal testing between these two conditions (Vansteenwegen et al., 2006). However, it would be unclear whether differences are due to an enhancing effect of X for conditioning or an attenuating effect of X for extinction on responding to the CS. Another possibility is to include a control condition in which a novel cue Y is presented during CS renewal testing, although then the novelty of Y may decrease the CR (e.g., due to distraction).

4.14 AAB renewal (B)

If both CS-US acquisition and extinction take place in context A, then testing in context B produces a higher CR to the CS than in context A.

Domains: Across species and Pavlovian as well as instrumental procedures but, but robustness variable.

AAB renewal is typically assessed by comparing to a group that receives acquisition, extinction and testing all in context A (AAA control group, as in the description of the phenomenon above) or acquisition in context A and extinction and test in context B (ABB control group), where B is usually familiar. The effect is similar to

disinhibition, as discovered by Pavlov (1927), in which the addition of a novel stimulus to a conditioned-and-extinguished stimulus leads to a return of conditioned responding. Hovland (1937) provided the first demonstration of disinhibition in human fear conditioning, by showing that switching off the room light after conditioning and extinction led to a return of skin conductance responses to the CS. Bouton and Ricker (1994) provided the first demonstration using contextual changes in a conditioned suppression preparation in rats. The AAB renewal effect has been investigated in various procedures and species including tentacle lowering in snails (Muñiz Moreno & Loy, 2023), conditioned taste aversion (Rosas et al., 2007) and instrumental learning (Bouton et al., 2011) in rats, and predictive learning in humans (Rosas & Callejas-Aguilera, 2006). The test in B usually reveals CR, but not always higher than at the end of extinction training (see e.g. Nihei et al., 2023 for social fear conditioning in humans).

Like other forms of renewal, AAB renewal is commonly interpreted as evidence that extinction does not reflect “unlearning” of previously acquired CS-US contingency knowledge, but rather the acquisition of supplementary information that co-exists with the previously acquired knowledge (see also Pavlov, 1927). However, the basic demonstration of AAB renewal relative to its typical AAA or ABB control conditions leaves room for alternative explanations, in particular, it may reflect learned or unlearned responses to context A or B rather than to the CS (for an overview and discussion, see Vervliet et al., 2013). However, unlike ABA and ABC renewal, investigation of potential context-based responding (or suppression of responding) is not often included in AAB renewal assays (Vervliet et al., 2013).

In conclusion, AAB renewal is not as widely or clearly demonstrated as ABA or ABC renewal effects, and while it could in principle provide a more decisive demonstration of

the context specificity of extinction to a CS than ABA or ABC renewal, this would require additional evidence to rule out the contribution of context-based responding.

4.15 Concurrent recovery (C)

After A-US acquisition and A-noUS extinction, B-US acquisition training leads to increased CR to A.

Domains: Rabbit eyeblink conditioning; only replicated within a single laboratory

See Table S2.

Concurrent recovery (ConRec) is usually assessed with A and B from different sensory modalities (Dudeney et al., 2007; Kehoe et al., 1995; Macrae & Kehoe, 1999; Weidemann & Kehoe, 2003, 2004, 2005). This ConRec effect was initially demonstrated in a so-called three-stage Pavlovian aversive conditioning procedure in rabbits (Kehoe et al., 1995).

To date, ConRec has only been demonstrated in rabbits in a series of studies (11 studies in total; 280 rabbits in total) conducted by one lab (Kehoe and associates), using the above-mentioned three-stage Pavlovian aversive conditioning procedure. The CSs were a tone and light, and the US was electric shock. The reported CR was the mean percent of trials on which animals emit a nictitating membrane response upon CS presentation. Within this specific species and procedure, ConRec appears to be a robust phenomenon: It is not affected by variations in the number or spacing of trials across stages (Macrae & Kehoe, 1999), or by variations in the number of extinction trials (Weidemann & Kehoe, 2003), nor is it influenced by different initial acquisition (Stage 1) procedures (Weidemann & Kehoe, 2005). ConRec has been observed in both between- and within-subjects designs, although only one experiment employed a within-subjects design (Weidemann & Kehoe, 2004).

Two boundary conditions can reduce the amount of ConRec: 1) Increasing the number of test trials in Stage 3 (Weidemann & Kehoe, 2005), and 2) increasing the number of CS2-US pairings in Stage 1 (Weidemann & Kehoe, 2004). Note that reinstatement (presentations of the US following extinction) may be a contributing factor to ConRec. One recent study investigated ConRec in conditioned taste aversion in rats and found no evidence for it (Michaud & Bouton, 2024).

Our C grading is based on the fact that this has been shown in one laboratory only. The median A grading in the survey was based on a very small number of 5 respondents.

4.16 Retrieval-extinction effect (C)

Following conditioning with a CS, extinction following retrieval of that CS alone reduces reinstatement, spontaneous recovery, and renewal, compared to standard extinction.

Domains: Appetitive Pavlovian conditioning in rodents, some evidence in aversive Pavlovian conditioning in rodents and humans, but there are considerable null and opposing findings without clear knowledge of the boundary conditions

To assess the *retrieval-extinction effect* extinction typically starts a few minutes after a brief re-presentation of that CS alone. Initially reported in rats (Monfils et al., 2009), the effect was soon also reported in mice (Clem & Huganir, 2010) and humans (Schiller et al., 2010). The retrieval-extinction effect is typically interpreted (often within the conceptual framework of *reconsolidation*) as an example of a more general conceptual model whereby presentation of a previously trained CS renders established memories about that CS labile under certain circumstances (Jardine et al., 2022).

While subsequent investigations reported mixed effects in both humans and rodents, an initial quantitative meta-analysis (Kredlow et al., 2016) provided only qualified support for the robustness of the effect. In particular, it suggested that the

evidence was consistent with no overall effect in rodents when using aversive stimuli (albeit there was a suggestion of moderating effects, such as housing conditions, although this in turn was partially confounded with the laboratories involved), a large overall effect in rodents with appetitive stimuli, and a moderate overall effect in humans when using aversive stimuli, and insufficient data to assess the effect in humans with appetitive stimuli. However, following this meta-analysis, pre-registered replications of the original rat (Luyten & Beckers, 2017) and human (Chalkia, Schroyens, et al., 2020) studies did not reproduce the initially reported effects, and a re-analysis of the original human data has raised questions regarding the adequacy of the original analysis (Chalkia, Van Oudenhove, et al., 2020).

These direct replication failures and other mixed results led a recent review (Jardine et al., 2022) to suggest that it was unclear whether pre-extinction presentation of a CS does or does not result in enhanced extinction. This review also considered the possibility that unknown moderators influenced whether or not pre-extinction presentation of the CS was sufficient to engage the reconsolidation mechanism(s) purported to underlie the retrieval-extinction effect, as well as other more clearly established memory retrieval effects. In summary, without further research it is not clear whether the retrieval-extinction effect lacks robustness, or subject to yet-to-be-discovered moderating effects that can explain why it has been reported inconsistently.

4.17 Secondary extinction (C)

After conditioning with A-US and B-US, extinguishing A also reduces CRs to B.

Domains: Mainly rat fear conditioning with intermixed CSs.

See Table S2.

Secondary extinction (SE) refers to the phenomenon that, after independent conditioning of two CSs, extinction of one CS attenuates CRs to the other CS that had not been subjected to extinction training (Pavlov, 1927; Vurbic & Bouton, 2011a).

SE was initially demonstrated by Pavlov in his seminal work with dogs (Pavlov, 1927). Afterwards, four published rat studies examined the phenomenon (Bouton & King, 1983; Kasproff et al., 1984; Ledgerwood et al., 2005; Vurbic & Bouton, 2011a) and only two of them demonstrated SE (Ledgerwood et al., 2005; Vurbic & Bouton, 2011a). All of these studies employed the same procedure, similar CSs, similar USs, and the same CR quantification (see Table S1 for more details). Hence, SE seems to have limited evidence of robustness and generalizability, and is subject to specific boundary conditions (see below). Among the four studies in rats, the one by Vurbic and Bouton (2011b) provided the most systematic investigation of SE and can be considered authoritative. No human studies examining SE have been published to date.

From the work of Vurbic and Bouton (2011b), it seems that SE is more likely to be observed in a conditioning procedure that encourages generalization between the CSs involved through association with a common temporal context, that is, intermixing multiple CSs during the conditioning phase.

4.18 Mediated extinction (C)

If two CSs have been presented together, non-reinforced presentation of one of them yields a reduction in responding to the other.

Domains: Widely observed but with highly variable results and unclear boundary conditions.

The term mediated extinction was coined by Holland and Forbes (1982) to describe the result of the following design (applied in this case to a conditioned taste aversion procedure in rats): A-B paired; A-US; B alone; test on A and observe a reduction

in responding to A as a result of B being presented without reinforcement compared to appropriate controls. To our knowledge, this “canonical” design has only been reported on one other occasion (Ward-Robinson & Hall, 1996) using rats and a conditioned suppression procedure. However, in a closely related design, AB-US; B without reinforcement; test on A, yielding a reduction in responding to A compared to appropriate controls, has been reported more frequently and across a wider variety of species (humans, rats, pigeons, and mice) and preparations (e.g., conditioned taste aversion, conditioned suppression, outcome prediction, and discriminated instrumental conditioning) (Liljeholm & Balleine, 2009; Rescorla, 1983; Reynolds & Reed, 2018; Shevill & Hall, 2004; Sissons et al., 2009; Stout & Miller, 2004; Thrailkill & Bouton, 2015).

However, the results reported from this design are highly variable, with many reports of either no change in responding to CS1 (Revusky et al., 1977) or an increase in responding (Liljeholm & Balleine, 2009; Reynolds & Reed, 2018; Shevill & Hall, 2004; Sissons et al., 2009; Stout & Miller, 2004) instead of a decrease. The source of this variability is hard to determine with certainty, but some procedural factors have been investigated: direct comparisons suggest that long CSs appear to favor the observation of mediated extinction over the opposite effect in both rats and humans (Reynolds & Reed, 2018; Sissons et al., 2009); mediated extinction is more commonly observed when similar as opposed to dissimilar CSs are employed (Liljeholm & Balleine, 2009); and simultaneous presentation of B and A as opposed to serial B->A presentation favors the observation of mediated extinction over the opposite effect in rats (Shevill & Hall, 2004) Thus, while the mediated extinction effect has been reported and can be observed across a variety of species and preparations, the factors determining when it is (or is not) observed are yet to be fully determined.

5 Inhibitory conditioning

5.3 Conditioned inhibition after differential conditioning (B)

After interspersed A-noUS presentations and B-US pairings, A reduces the CR when paired with a US-predictive C (summation test), and when A is paired with the US, acquisition of the CR is retarded (retardation test).

Domains: Eyeblick conditioning and lick suppression in rats; autonomic conditioning in humans

Conditioned inhibition produced through differential conditioning (A-noUS / B-US) as revealed by summation and retardation tests has been observed, for example, with eyeblink conditioning (Campolattaro et al., 2008) and conditioned lick suppression (R. R. Miller et al., 1991a; Urcelay & Miller, 2006) in rats, and skin conductance changes in humans (Grings et al., 1974).

For both summation and retardation measures, conditioned inhibition after differential conditioning appears to be more likely with massed rather than spaced trials (Urcelay & Miller, 2006). Moreover, the amount of differential conditioning resulting in evidence for conditioned inhibition on a retardation test can be insufficient to reveal conditioned inhibition on a summation test (Campolattaro et al., 2008).

Urcelay and Miller (2006) have reported data suggesting that negative contingency training and differential conditioning are both essentially a variant of simultaneous feature-negative inhibition in which the training context plays the role of stimulus B.

That effect sizes for evidence of conditioned inhibition are moderate or small is not surprising given that all procedures for establishing a conditioned inhibitor are dependent on the excitatory strength of the conditioned stimulus (B or the training context) that is used in the treatment used to create the conditioned inhibitor.

Our B grading is based on the limited number of procedures in which this has been observed. We note that the AA median grading in the survey is based on a small number of 6 respondents.

5.4 Extinction resistance of conditioned inhibition (B)

After interspersed A-noUS presentations and B-US pairings, A reduces the CR when paired with a US-predictive C (summation test), and when A is paired with the US, acquisition of the CR is retarded (retardation test).

Domains: Conditioned suppression in rats, human predictive learning

After establishing conditioned inhibition, repeated presentations of the conditioned inhibitor alone without the US usually fail to decrease its inhibitory properties. This finding has been documented, for example, in conditioned suppression with rats (Zimmer-Hart & Rescorla, 1974) and human predictive learning (Melchers et al., 2006). However, the failure to extinguish inhibition by non-reinforced presentations of the inhibitor alone seems to depend on features of the stimulus used as the US. In situations in which the US can appear in two opposing forms (e.g., increase or decrease of a value), presentations of a conditioned inhibitor alone without the US (no value change) lead to a decrease in the potential of the conditioned inhibitor to pass the two tests for conditioned inhibition (Lotz & Lachnit, 2009; Melchers et al., 2006). Thus, the resistance to extinction of conditioned inhibitors appears to be procedure-specific.

5.5 Retrospective revaluation of conditioned inhibition (C)

After interspersed AB-noUS presentations and B-US pairings, further B-US presentations increase, and B-noUS presentations reduce, the conditioned inhibitory properties of A in summation and retardation tests.

Domains: Conditioned suppression in rats

Repeated B-noUS presentations after conditioned simultaneous feature-negative discrimination reduce the inhibitory potential of A as revealed by summation and retardation tests (R. R. Miller et al., 1991b). In contrast, the administration of additional B-US pairings enhances conditioned inhibition of A as measured in summation and retardation tests (Amundson et al., 2005). Both studies come from the same laboratory and used the same conditioned lick suppression procedure; the generality of this phenomenon thus requires further investigation.

6 Stimulus competition/potential

6.4 Relative validity (B)

The CR to CS A is weaker when training consists of AB-US pairings alternated with AC-noUS trials than when it consists of AB trials alternated with AC trials, with each type reinforced half of the time.

Domains: Conditioned suppression, taste aversion, magazine-approach conditioning (all rats); eyeblink conditioning (rabbits); autoshaping (pigeons) with no systematic investigation of procedural variation

This phenomenon was first reported by Wagner et al. (1968) using conditioned suppression in rats. This effect has also been observed in eyeblink conditioning in rabbits, in taste aversion learning in rats (Luongo, 1976), magazine-approach conditioning in rats (Mondragón & Murphy, 2010), and autoshaping in pigeons (Wasserman, 1974), as well as in humans (Baetu et al., 2005; Callejas-Aguilera & Rosas, 2010b). However, there are reports of failures to see the relative validity effect (e.g., Quigley & Haselgrove, 2023, in human predictive learning).

6.5 Overexpectation (B)

Reinforced AB presentations following independent reinforced presentations of A and B result in a decrement in the CR to A and B separately.

Domains: Multiple procedures in multiple species, but only few demonstrations and negative results

Overexpectation has been observed using conditioned suppression (Rescorla, 1970), conditioned freezing (McNally et al., 2004, p. 200), and appetitive Pavlovian and instrumental conditioning in rats (Lattal & Nakajima, 1998), autoshaping in pigeons (Khallad & Moore, 1996), eyeblink conditioning in rabbits (Kehoe & White, 2004), olfactory conditioning in crickets (Terao et al., 2022), and causal learning in humans (Collins & Shanks, 2006). However, overexpectation is not ubiquitous, with reported failures to observe it using conditioned suppression in rats (St. Claire-Smith & Mackintosh, 1974). The effect size is typically small.

Our B grading is based on the limited number of narrowly defined procedures and unclear boundary conditions. However, it is widely known and discussed in many introductory textbooks, which we suggest might explain the AA median grading in the community survey.

6.6 Unblocking by increasing (or decreasing) the US (B)

Increasing (or decreasing) the US between A training in Phase 1 and AB training in Phase 2 increases responding to the blocked B.

Domains: Conditioned suppression and appetitive Pavlovian conditioning in rats, autoshaping in pigeons

Unblocking refers to reducing the response deficit of forward blocking by increasing (or decreasing) the US between the A-US phase and the AB-US phase of treatment. Increases in US intensity (Bakal et al., 1974; Kamin, 1969) or number (C. Y.

Chang et al., 2017; Dickinson et al., 1976) increased responding to the blocked B by rats. Decreases in US number (Dickinson et al., 1976) but not intensity (Wagner et al., 1980) increased responding to the blocked B also in rats. Khallad and Moore (1996) reported similar effects in pigeons.

6.7 Backward blocking (B)

When AB-US pairings in Phase 1 are followed by A-US pairings in Phase 2, the CR to B is weaker than without the A-US pairings.

Domains: Conditioned suppression in rats, contingency judgements in humans

The backward blocking procedure is the same as forward blocking, but with phases 1 and 2 in reverse order. This has been demonstrated in human contingency judgements (Shanks, 1985) and conditioned suppression in rats (Pineño et al., 2005; Urushihara & Miller, 2010). Backward blocking is more apt to be seen when the outcome is not biologically significant, which might explain some of the non-replications of this phenomenon (R. R. Miller & Matute, 1996).

6.8 Unequal changes in responding by elements as a result of compound pairings (compound conditioning) (B)

Unequal changes in CR to two CSs trained in compound occur when the CSs start with different response potentials.

Domains: conditioned suppression, magazine approach, instrumental learning in rats and pigeons, but only few demonstrations

Rescorla initially reported this phenomenon in rats and pigeons (Rescorla, 2000, 2001, 2006). With rats, he demonstrated it in instrumental discriminative learning, conditioned suppression, and US approach (i.e., goal tracking), and in pigeons, he did so in CS approach (i.e., sign tracking). The effect has been observed when initially one CS is

excitatory, the other is inhibitory, and their compound is reinforced (Rescorla, 2000); when initially one CS is excitatory, the other is neutral, and their compound is reinforced (Rescorla, 2001). A similar effect occurs with compound non-reinforcement: here the cues have been conditioned and then partially extinguished prior to their compound being non-reinforced (Rescorla, 2006). Unequal learning effects have also been observed by a different laboratory in a rat conditioned suppression procedure (Fam et al., 2017), and in human predictive learning (Spicer et al., 2022). This phenomenon seems to have a medium effect size.

6.9 Recovery from overshadowing (B)

Extinction of the overshadowing cue results in increased responding to the overshadowed cue.

Domains: Conditioned suppression in rats; human causal judgement

Following overshadowing treatment (i.e., AB-US) that has attenuated responding to B relative to a B-US control condition, several different treatments have been reported to result in increased responding to B (i.e., decreased overshadowing). This has been shown for extinction of A, using conditioned suppression in rats (Kaufman & Bolles, 1981) and contingency learning in humans (Wasserman & Berglan, 1998), presentations of the US alone using conditioned suppression in rats (Kasprow et al., 1982), and longer retention intervals using taste aversion in rats (Kraemer et al., 1988). However, small changes in procedural variables appear to influence these observations. For example Holland (1999) did not observe recovery from overshadowing after extinguishing the overshadowing cue. There has been no systematic investigation of procedural variation.

6.10 Overshadowing is stronger than external inhibition (B)

Adding a CS to a trained compound of two CS results in a smaller decrease in CR than does removing a CS from the same compound.

Domains: Rabbit eyeblink conditioning, rat fear conditioning, human predictive learning

This phenomenon describes the asymmetry in generalization decrement when adding a novel cue to a trained element or compound (external inhibition, see benchmark 2.5) compared to subtracting a trained cue from a trained compound (overshadowing, see benchmark 6.1). Specifically, subtracting a trained cue results in a larger generalization decrement than adding a novel cue. Pavlov (1927), using his salivation preparation in dogs, first noted that either adding or subtracting a stimulus resulted in some degree of generalization decrement. The first demonstration of the asymmetry in this decrement was reported by Brandon et al. (2000), who used an eyeblink conditioning procedure in rabbits.

This asymmetry in generalization decrement has also been demonstrated in rats and humans. González (2003) found the asymmetry in generalization decrement in rats using fear conditioning with stimuli from different modalities (tone/light/odor). Glautier (2004) demonstrated the effect in two human predictive learning experiments where the stimuli were the visual features of a plane and the outcome was low/high pollution. Wheeler et al. (2006) demonstrated the effect in two human predictive learning experiments with discrete foods as stimuli and food poisoning as the outcome. Thorwart and Lachnit (2010c) found the asymmetry in predictive and causal learning scenarios, and separate and grouped stimulus configurations. Thus, in humans, the effect does not seem to depend on the presentation of the stimuli as discrete or configural. Although there are

limited published studies, the majority show the effect, suggesting replicability across laboratories (Soto et al., 2014).

Thorwart and Lachnit (2009b) reported null findings (symmetrical generalization decrement) in three human predictive learning experiments using different manipulations of movement and spatial location of the stimuli (colored dots presented on screen). These experiments were similar to Thorwart and Lachnit (2010c) in design and stimuli, and therefore it is not clear what the determining factor was for these conflicting results.

6.11 Redundancy effect (B)

Stronger responding to the blocked stimulus B after A-US/AB-US pairings than to an irrelevant stimulus B after AB-US/BC-noUS pairings.

Domains: Magazine approach in rats, predictive learning in humans

The redundancy effect has been reported in magazine approach by rats (Pearce et al., 2012) and in several human predictive learning tasks (Beesley & Le Pelley, 2011; Le Pelley et al., 2014; Uengoer et al., 2013, 2019). Thus, the effect appears to generalize across at least some tasks and species, but further research is needed to determine its generality and boundary conditions.

6.12 Recovery from forward blocking (C)

Several different post-blocking manipulations result in increased responding to the blocked cue.

Domains: conditioned suppression in rats

Increased responding to a blocked stimulus B (i.e., decreased blocking) has been reported as a result of extinction of the blocking stimulus A (Blaisdell et al., 1999), a change in the test context from that of A-US training (Miguez & Miller, 2022), longer

retention intervals (Pineño et al., 2005), and presentation of the US alone after Phase 2 of blocking (Balaz et al., 1982). All of these examples used conditioned suppression by rats and were conducted in the same laboratory, so there is a need for tests of generality across laboratories, tasks and species.

6.13 Recovery from backward blocking (C)

Extinction of the blocker A results in increased responding to the blocked B.

Domains: Conditioned suppression in rats

After backward blocking treatment (AB-US followed by A-US trials), increased responding to the backward blocked cue B has been reported as a result of testing in a context different from that of A-US treatment (Miguez & Miller, 2022) and longer retention intervals (Pineño et al., 2005). Both demonstrations used conditioned suppression by rats and come from the same laboratory, so generality across laboratories, tasks and species still needs to be assessed.

This phenomenon received an A median grading in the survey. In contrast, backward blocking itself, on which this phenomenon builds, was only graded B in the survey, which appears inconsistent.

7 CS/US pre-exposure effects

7.5 Context pre-exposure facilitates aversive CRs to the context (B)

Domains: Rat contextual conditioning with shock or nausea US

See Table S2.

Pre-exposure to the environmental cues (context) where a foot shock will later serve as a US can either enhance fear conditioning to that context (Kiernan & Westbrook, 1993b), although under specific conditions, the opposite is observed.

Facilitation of contextual fear conditioning by context pre-exposure is demonstrated by comparing it to a group with no pre-exposure, for which context conditioning is typically minimal or absent, a phenomenon known as the "immediate shock freezing deficit" (Fanselow, 1986). The freezing CR increases with longer intervals between placement in the environment (T1) and the shock (T2) (Fanselow, 1986). Additionally, fear conditioning improves with more pre-exposures to the shock context (1 vs. 4 exposures), but only when the pre-exposures are brief (2 vs. 20 minutes) (Kiernan & Westbrook, 1993a).

When a long T1-T2 interval (81 seconds) was combined with prolonged pre-exposures (four 20-minute sessions), fear conditioning was reduced instead of enhanced, seemingly an example of LI of the context (Kiernan & Westbrook, 1993a). This reduction also occurs with longer T1-T2 intervals, reflecting an inverted U-shaped relationship in the fear response (R. Westbrook et al., 1994). Furthermore, the effect is influenced by the intensity of the US; a higher intensity US eliminates the immediate shock freezing deficit, resulting in similar levels of fear conditioning between pre-exposure and non-pre-exposed groups (Bevins et al., 1997).

The facilitation of fear conditioning due to pre-exposure to the context has been mainly reported in studies involving rats and mice, using shocks and lithium chloride injection as the US. However, this effect has not been replicated in humans. For instance, Tröger (2012) found no evidence that pre-exposure to the to-be-conditioned context either enhances or impairs context conditioning in a virtual reality task, contradicting findings from animal studies.

7.6 Hall–Pearce effect (B)

Training CS–weak US leads to slower acquisition of CS–strong US.

Domains: Aversive Pavlovian conditioning in rats.

Repeated pairings of a CS with a weak US lead to slower subsequent acquisition of an association between that CS and a stronger US (Hall & Pearce, 1979). This effect is attenuated if unreinforced presentations of the CS are inserted between the training stages (Hall & Pearce, 1982). The Hall-Pearce effect has been replicated multiple times in aversive conditioning using rats as subjects (Ayres et al., 1984; e.g., Hall & Pearce, 1982; Kaspro et al., 1985; Rodríguez & Alonso, 2011; Savastano et al., 1998; Young & Fanselow, 1992). In contrast, experiments with eyeblink conditioning in rabbits have not observed the effect (Ayres et al., 1984), suggesting that it might depend on the particular procedure or species.

7.7 Learned irrelevance (B)

Random interspersed presentations of the CS alone and the US alone retard conditioning even more than combined latent inhibition and US pre-exposure.

Domains: Robust across species, but with a limited range of Pavlovian procedures

See Table S2.

When presentations of a CS and a US are uncorrelated, such that one does not predict the occurrence of the other, subsequent acquisition of excitatory or inhibitory conditioning is retarded (Mackintosh, 1973). This phenomenon, termed *learned irrelevance*, has been shown to yield greater retardation of conditioning than the combined effects of independent pre-exposure to the CS and the US.

Learned irrelevance has been documented across various experimental procedures and species, including eyeblink conditioning in rabbits and humans (e.g., Allen et al., 2002), conditioned lick suppression in rats (e.g., A. G. Baker & Mackintosh, 1977), fear conditioning (A. Baker et al., 2003), and appetitive conditioning in rats (e.g., C. Bennett et al., 1995; C. H. Bennett et al., 2000), as well as contingency/predictive judgments in humans (e.g., C. E. Myers et al., 2000). Table S2 provides a more detailed

overview. However, relatively few studies have shown that uncorrelated CS/US exposure leads to greater retardation than the sum of pre-exposure to the CS and US. Some research has reported greater retardation, such as in rats' conditioned emotional and appetitive conditioning, with corroboration (C. Bennett et al., 1995) of the original result in magazine approach. A substantial number of studies have compared uncorrelated pre-exposure of the CS and US with pre-exposure with CS alone or US-alone pre-exposure. While these studies reported greater retardation in learning in the uncorrelated condition, they did not include a combined CS and US pre-exposure control. Bonardi and Hall (1996) found boundary conditions for this greater retardation. They observed slower conditioning when the procedure involved multiple trials, but found the opposite result when conditioning involved a single trial. Expanding on these boundaries, (Maldonado et al., 1999) found that non-contingent experience impaired the detection of a positive contingency and facilitated the detection of a negative contingency in a human contingency task, a result later corroborated in rats (Bonardi et al., 2005).

We have not identified evidence of learned irrelevance in instrumental conditioning, and indeed it remains unclear how such a procedure could be implemented in a situation where the animal is free to respond or not respond. A procedurally somewhat related phenomenon, however, might be learned helplessness (Maier & Seligman, 2016).

7.8 Following CS-pre-exposure and conditioning, a long relative to a short delay before testing decreases CRs (super latent inhibition) (C)

Domains: Rat conditioned taste aversion and conditioned suppression, human predictive learning

See Table S2.

A LI (see benchmark 7.1) procedure typically consists of a three-stage design: pre-exposure (CS alone), conditioning (CS-US), and testing. In this procedure, a long delay before the final test, spent outside the conditioning context, further reduces the CR compared to a short delay (Super-LI, see review in Lubow & De La Casa, 2005).

The increase in LI (reduction of the CR) with delay has been demonstrated primarily in rats' conditioned taste aversion using sodium saccharin as a CS, and a 0.5% body weight intraperitoneal injection of an emetic (0.4M lithium chloride) as the US. The phenomenon has also been reported in conditioned taste preference (e.g., De La Casa & Lubow, 2000a), conditioned suppression in rats (e.g., Wheeler et al., 2004), and human probability judgments (Stout et al., 2005). The most common retention intervals with rats are 1 and 21 days for short and long intervals, respectively. In the human study, testing was conducted either immediately or 48-h after cue-outcome pairings.

De La Casa and Lubow (2002) manipulated the number of flavor exposures (0, 2, 4), the length of the retention interval (1, 7, 14, or 21 days), and its placement (between pre-exposure and conditioning or between conditioning and testing. De la Casa and Lubow. De la Casa and Lubow (2000b) also manipulated US intensity and the location of the retention interval (same or different from where the treatments were conducted). Super-LI was observed only after four CS exposures, a 21-day retention interval, and when the retention interval was spent in a location different from where the treatments were administered. When the retention interval was spent in the same room as the treatments (a common practice in conditioned taste aversion studies), the effect consistently reported is an attenuation, rather than an enhancement, of LI (e.g., McIntosh & Tarpy, 1977). However, Best and Gemberling (1977) found an increase in LI when the pre-exposure/conditioning interval was spent in the experimental room for up to 3.5 hours. In contrast, Rosas and Bouton (1997) found that a 28-day pre-

exposure/conditioning interval attenuated LI when it was spent outside the experimental rooms. These findings suggest that both the temporal placement of the retention interval in the design, and where the interval is spent, are key boundary conditions for observing super-LI. More research is needed to illuminate the critical variables.

7.9 Presentation of a different CS before conditioning disrupts latent inhibition (C)

Domains: Conditioned suppression and conditioned taste aversion in rats; contingency/predictive judgments in humans

See Table S2.

LI (see benchmark 7.1) is reduced when a non-target affectively-neutral stimulus is presented soon before conditioning. This effect was first observed in rats using a conditioned suppression procedure with tone and light as stimuli (Lantz, 1973) and later in conditioned flavor aversion using vinegar as the CS and vanilla as an interpolated distractor (Best et al., 1979). Human studies have also corroborated this effect, including one study that used a masking task and reported attenuation of LI when a novel stimulus was introduced between pre-exposure and conditioning (Pineño et al., 2006). See table S2 for a detailed overview.

However, the effect has not been observed in human fear conditioning (Lipp & Vaitl, 1992). Additionally, Leung (2013) measuring freezing instead of conditioned suppression, found that introducing a different CS during the interposition phase deepened, rather than attenuated, LI, suggesting that the effect is subject to boundary conditions that remain unclear.

7.10 Recovery from latent inhibition (LI) induced by context extinction (C)

LI is attenuated by extensive exposure to the training context between CS pre-exposure and the CS-US pairings or between the CS-US pairings and testing.

Domains: Conditioned suppression and conditioned taste aversion in rats; predictive learning in humans; robustness unclear

See Table S2.

LI is attenuated by extensive exposure to the training context after CS pre-exposure. This was first observed in rats using a conditioned suppression procedure with a clicker as the CS, food pellets as reinforcers, and a foot shock as the US. This effect occurred only when context exposure was conducted with on-baseline bar press training (A. G. Baker & Mercier, 1982). It was later observed in conditioned lick suppression with off-baseline context extinction either between CS pre-exposure and the CS-US pairings or CS-US pairings and testing (Grahame et al., 1994), and in a sensory preconditioning (CS-CS pairings) with extensive context exposure between pre-exposure and acquisition (Gunther et al., 1997).

Hall and Minor (1984) did not find attenuation of LI by context exposure in rats using a conditioned suppression, regardless of whether lick suppression or bar-press suppression was measured. Neither extensive context exposure nor an explicit Context-CS negative correlation introduced between pre-exposure and conditioning impacted LI more than the simple delay. The null effect of context exposure has also been reported in human predictive learning, although only 120 min of context exposure between acquisition and testing was used (Zalstein-Orda & Lubow, 1995). Additionally, in context taste aversion, long exposure to the experimental context between CS-US pairings and testing does not affect LI, while the same delay spent in a different context increases LI (super-LI effect). Overall, while the effect of context exposure on LI is theoretically relevant and has repeatedly been demonstrated, there are conflicting findings, and the boundary conditions have not been established.

While our C grading is based on limited demonstrations, it received a median grade of A in the survey, albeit based on a small number of raters ($N = 6$).

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