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Elaboration of a model of Pavlovian learning and performance: HeiDI

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Abstract

The model elaborated here adapts the influential pooled error term, first described by Allan R. Wagner and his colleague Robert A. Rescorla, to govern the formation of *reciprocal associations* between any pair of stimuli that are presented on a given trial. In the context of Pavlovian conditioning, these stimuli include various conditioned and unconditioned stimuli. This elaboration enables the model to deal with cue competition phenomena, including the relative validity effect, and evidence implicating separate error terms and attentional processes in association formation. The model also includes a performance rule, which provides a natural basis for (individual) variation in the strength and nature of conditioned behaviors that are observed in Pavlovian conditioning procedures. The new model thereby begins to address theoretical and empirical issues that were apparent when the Rescorla-Wagner model was first described, together with research inspired by the model over ensuing 50 years.

Keywords: Associative learning, reciprocal associations, pooled error term, performance

The ideas embodied in the formal models of associative learning proposed by Allan R. Wagner and his colleagues, together with the empirical research upon which they were founded, have provided the inspiration for much of the work conducted in the fields of animal learning, human learning and behavioral neuroscience for over 50 years. In fact, the impact of the formal model of Pavlovian conditioning that he developed with Robert A. Rescorla (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972) was immediately apparent: The final chapter of *Mechanisms of Animal Discrimination Learning* presents a detailed evaluation of the model, which was 'in press' in 1970 (pp. 464-502; Sutherland & Mackintosh, 1971). The new model was the perfect counterpoint to the views of Sutherland and Mackintosh: While they pursued the idea that the process of discrimination learning involved changes in attention to stimuli or stimulus dimensions, Rescorla and Wagner assumed that learning was determined by variation in the effectiveness of reinforcement and nonreinforcement. The core set of phenomena that motivated these important departures from the theoretical analyses offered by Hull (1943) and Spence (1937) represents the foundation of contemporary learning theory. We will first provide a synopsis of the Rescorla-Wagner model, before turning to a recent elaboration of it (HeiDI; Honey, Dwyer & Iliescu, 2019). This elaboration addresses theoretical and empirical issues that were apparent when the Rescorla-Wagner model was first described, together with some of the research inspired by the model over intervening 50 years. The name HeiDI reflects the surnames of the authors, and echoes the integrated form of Johanna Spyri's book, which was originally presented as two companion pieces: *Heidi: Her years of wandering and learning*, and *Heidi: How she used what she learned*.

The Rescorla-Wagner Model

$$\Delta V_{CS\text{-}US} = \alpha_{CS}.\beta_{US}(\lambda - \Sigma V_{TOTAL\text{-}US}) \quad (0)$$

The model assumes that Pavlovian conditioning involves the formation of an association between the conditioned stimulus (CS) and unconditioned stimulus (US); and that associative strength (V) is monotonically related to the strength of conditioned responding. The change in the associative strength ($\Delta V_{CS\text{-}US}$) of a CS on a given trial is determined by the difference between the maximum associative strength supportable by a US (λ) and the pooled associative strength of all stimuli presented on that trial ($\Sigma V_{TOTAL\text{-}US}$). The adoption of a pooled error term (i.e., $\lambda – \Sigma V_{TOTAL\text{-}US}$) allows the model to accommodate phenomena (blocking; e.g., Kamin, 1969; conditioned inhibition; e.g., Rescorla, 1969; contingency effects; e.g., Rescorla, 1968; overshadowing; e.g., Mackintosh, 1978; relative validity; e.g., Wagner, 1969; Wagner, Logan, Haberlandt, & Price, 1968; superconditioning; e.g., Rescorla, 1971) that were beyond the scope of models with separate error terms for each component of a pattern of stimulation (e.g., Bush & Mosteller, 1951; Hull, 1943; Spence, 1937). The use of the pooled error term means that $\Delta V_{CS\text{-}US}$ is affected not only by the current associative strength of that stimulus (i.e., $V_{CS\text{-}US}$), but also by the presence of other stimuli with associative strength (i.e., by $\Sigma V_{TOTAL\text{-}US}$). The change in associative strength driven by the pooled error term is modulated by the product of two learning rate parameters, α_{CS} and $\beta_{US,}$ which were aligned to the salience of the CS and US, and confined to the unit interval: $0 \leq \alpha_{CS,}\ \beta_{US} \leq 1$. To enable inhibitory learning to occur, on trials when the US is absent, Rescorla and Wagner (1972; see also Wagner & Rescorla, 1972) assumed that β takes a positive value on such trials when the CS is present, while λ is set to 0. In fact, they were forced to suppose that this positive value for β was lower on nonreinforced trials than reinforced values in order to provide an account of the relative validity effect (Wagner et al., 1968).

The Relative Validity Effect

The relative validity effect was one of the phenomena that provided the impetus for the adoption of a pooled error term. The essential features of the elegant experimental design used by Wagner et al. (1968) are summarized in Table 1. All animals received training trials with a target stimulus (A) that was paired with a reinforcer on 50% of trials (denoted +) and was nonreinforced on the remaining trials (denoted –). However, for animals in the true discrimination group, when A was reinforced it was always accompanied by B (on AB+ trials) and when A was nonreinforced it was always accompanied by C (on AC– trials). In contrast, for animals in the pseudo discrimination group, presentations of AB and AC were equally often reinforced and nonreinforced (AB+/– and AC+/–). Thus, while the individual reinforcement history of A was the same in the two groups, the correlation of B and C with reinforcement and nonreinforcement differed. During the critical test trials, A, B and C were presented individually. As expected, in the true discrimination group, the presentation of B elicited considerably more conditioned responding than C, whereas in the pseudo-discrimination group, B and C elicited levels of responding that were intermediate to these stimuli in the true discrimination group. These observations merely reflect the fact that while B signaled reinforcement and C nonreinforcement for animals given the true discrimination, for those given the pseudo discrimination B and C were equally often reinforced and nonreinforced. The critical finding was that A elicited less responding in the true discrimination group than in the pseudo-discrimination group.

Table 1. The relative validity design

True discrimination:	AB+	AC–
Pseudo discrimination:	AB+/–	AC+/–

Note: A, B and C denote conditioned stimuli, and + and – represent reinforcement (+) and nonreinforcement (–).

It is a simple matter to apply the Rescorla-Wagner model to the development of excitatory associations on the reinforced trials in the two groups: Because B is always reinforced in the true discrimination group it will acquire appreciable excitatory associative strength, which will limit the development of the associative strength of A when it is reinforced on AB+ trials; and because B (and C) are inconsistently reinforced in the pseudo discrimination group, there is more scope for A to gain excitatory associative strength on reinforced AB and AC trials than in the true discrimination group. A moment's reflection, however, reveals that if one were to apply the same analysis to nonreinforced trials, then A should also lose less associative strength on these trials in the true discrimination group than in the pseudo discrimination group: Because C is consistently nonreinforced in the true discrimination group, it should limit the loss in the associative strength of A to a greater extent in the true discrimination group than in the pseudo discrimination group. Other things being equal, these two effects should cancel one another out, and leave A with equivalent associative strength in the two groups.

This observation forced Rescorla and Wagner (1972) to assume that the rate of learning generated by reinforcement (e.g., on AB+ trials) was greater than the loss in associative strength based on nonreinforcement (e.g., on AC– trials). This assumption means that group differences in the capacity of B to restrict the growth in the associative strength of A on reinforced trials has a greater impact than group differences in the capacity of C to restrict the loss in this strength on nonreinforced trials. This assumption was implemented by setting β to a higher value on reinforced than nonreinforced trials. This assumption is not implausible, but is it necessary? There is a related feature of the model that has not been questioned. Namely, is it necessary to have two separate parameters linked to the properties of the US: one that determines the learning rate (β_{US}) and the other that determines the asymptotic strength of the association that it can support (λ)? We will outline a new model, HeiDI, and show how it provides an account of the relative validity effect without the need to assume that there are: (i) different learning rates associated with reinforcement and nonreinforcement, or (ii) different parameters for the learning rate and asymptote for a given reinforcer. We then proceed by showing how HeiDI, which implements different versions of a pooled error term, also provides an analysis for evidence that has been taken to suggest the operation of separate error terms (e.g., Rescorla, 2000, 2001ab; see also, Allman & Honey, 2005; Allman, Ward-Robinson & Honey, 2005) and attentional processes (e.g., Dickinson, Hall, & Mackintosh, 1976) in association formation.

HeiDI: Learning rules

The key assumption of HeiDI is that reciprocal associations are acquired between any pair of stimuli that are presented on a given trial: between any pair of CSs, and between the CS and US. When this assumption is combined with the idea that the formation of each association is determined by a pooled error term, the resulting model has considerable explanatory power, especially when coupled with appropriate performance rules. The reciprocity assumption is consistent with evidence from a variety of sources, and with the trial-based updating of associative strengths, which is a feature both of the Rescorla-Wagner model and other influential models (e.g., Mackintosh, 1975; Pearce, 1994; Pearce & Hall, 1980). Indeed, in typical Pavlovian conditioning procedures, where a CS precedes but does not co-exist with the US, the memory trace of the CS must be sufficient to support the development of excitatory (reciprocal) associations (cf. Wagner, 1981). There is evidence that such reciprocal associations are acquired during forward conditioning in a variety of preparations (e.g., Arcediano, Escobar, & Miller, 2005; Asch & Ebenholtz, 1962; Cohen-Hatton, Haddon, George, & Honey, 2013; Gerolin & Matute, 1999; Honey & Bolhuis, 1997; Honey & Ward-Robinson, 2002; Rescorla & Freberg, 1978; Zentall, Sherburne, & Steirn, 1992). There is also complementary research on the conditions under which US-CS pairings result in conditioned responding to the CS (e.g., Ayres, Haddad, & Albert, 1987; Barnet & Miller, 1996; Cole & Miller, 1999; Heth, 1976; Matzel, Held, & Miller, 1988; Tait & Saladin, 1986). However, it should be acknowledged that presenting a US sometime before a CS can generate inhibitory learning involving that CS (e.g., Ewing, Larew, & Wagner, 1985; Honey, 1996; Tait & Saladin, 1986). While the introduction of an interval between the US and CS would reduce the opportunity for US-CS (and CS-US) associations to form, the development of inhibition could have a number of origins. For example, the experimental context might have sufficient (momentary) excitatory strength to generate inhibitory learning involving the CS. Indeed, even if β_{US} had simply decayed to a lower value at the point when the CS was presented, the excitatory associative strength of the context might be sufficient to generate such inhibitory learning (e.g., Cotton, Goodall, & Mackintosh, 1982; Nelson, 1987).

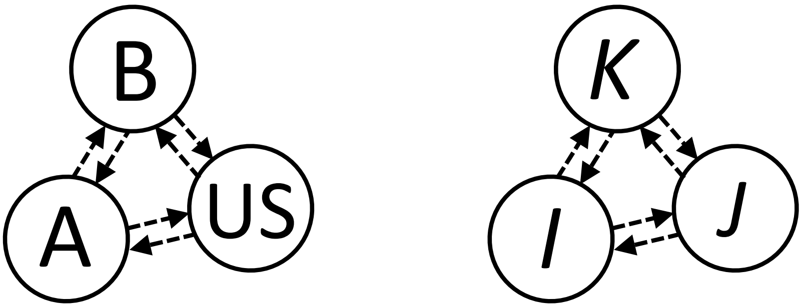
Equations 1 and 2 are the rules for determining the formation of reciprocal associations between a CS and US during simple Pavlovian conditioning; although the rules can be generalized to any pair of stimuli (see Figure 1). Thus, when considering a conventional CS-US pairing, in which the CS precedes the US, changes in associative strength of the reciprocal associations ($\Delta V_{CS\text{-}US}$ and $\Delta V_{US\text{-}CS}$) are determined by the value of the learning rate parameters for the CS (α_{CS}) and US (β_{US}) multiplied by the respective pooled error terms: ($c.\beta_{US} - \Sigma V_{TOTAL\ US}$) and ($c.\alpha_{CS} - \Sigma V_{TOTAL\ CS}$). $\Sigma V_{TOTAL\ US}$ and $\Sigma V_{TOTAL\ CS}$ represent the aggregate associative strengths of the stimuli that are present on a given trial with respect to the subscripted, target stimulus (i.e.., $_{US}$ and $_{CS}$, respectively). In both equations, the learning rate parameters (α_{CS} and β_{US}) are confined to the unit interval: $0 \leq \alpha_{CS}, \beta_{US} \leq 1$; and both are aligned to the (perceived) salience of the stimuli. We use the term perceived salience to emphasize our assumption that the salience of a given stimulus (CS or US) can vary between different animals, and in this way provide the basis for an analysis of individual differences in both the strength and nature of conditioned responding (e.g., Iliescu, Hall, Wilkinson, Dwyer, & Honey, 2018; Patitucci, Nelson, Dwyer & Honey, 2016). This analysis will be described later.

Returning to Equations 1 and 2, it should be noted that α_{CS} and β_{US} are dimensionless scalars, but when they serve as the asymptotes for associative strength they are multiplied by a constant (c). In order for the equations to be dimensionally balanced, c is required to have units of V. However, the numeric value of c is not set by this requirement. Here, we assume that c = 1 in units of V, which means that $c.\alpha_{CS}$ and $c.\beta_{US.}$ will be confined to the unit interval: $0 \leq c.\alpha_{CS}, c.\beta_{US} \leq 1$. But, it remains an option for c to take values greater or less than 1 in units of V and in that way for the asymptotic limits of learning to be a multiple of β_{US} in Equation 1 or α_{CS} in Equation 2. In any case, when the CS is absent α_{CS} and $c.\alpha_{CS}$ are set to 0 and when the US is absent β_{US} and $c.\beta_{US}$ are set to 0. In both equations, learning ceases when the aggregated associative strengths (e.g., $\Sigma V_{TOTAL\ US}$) equals the asymptote determined by the target of the association (e.g., $c.\beta_{US}$). In this way, Equations 1 and 2 provide a simple integrated analysis for how reciprocal associations form between two stimuli, with the values of α_{CS} and β_{US} determining both the rate at which associations are formed and the asymptotes that are reached. It should be clear, that if the CS were to be presented alone following CS-US pairings, then Equation 1 would return negative values, which could be aligned with either the simple loss of excitation (cf. Rescorla & Wagner, 1972) or the formation of a separate negative or inhibitory association between the CS and the absence of the US (cf. Konorski, 1967; Pearce & Hall, 1980; Zimmer-Hart & Rescorla, 1974). It should be equally clear, that such an extinction treatment would produce no equivalent change in the reciprocal US-CS, because the learning rate parameter β_{US} will be 0.

$$\Delta V_{CS\text{-}US} = \alpha_{CS}\left(c.\beta_{US} - \Sigma V_{TOTAL\text{-}US}\right) \quad (1)$$

$$\Delta V_{US\text{-}CS} = \beta_{US}\left(c.\alpha_{CS} - \Sigma V_{TOTAL\text{-}CS}\right) \quad (2)$$

We can now apply Equations 1 and 2 to the case in which a compound consisting of two stimuli (e.g., a tone and a light; A and B) is paired with a US (e.g., a food pellet). Under these conditions, six associations will be updated on a given trial: A-B, B-A, A-US, US-A, B-US and US-B (see Figure 1). If we consider the generalized forms of Equations 1 and 2 in Figure 1, then the development of an association between any stimulus (e.g., A) and another (e.g., the US), the change in associative strength (e.g., $\Delta V_{A\text{-}US}$) will be determined by the value of the learning rate parameter of the stimulus (e.g., α_A) multiplied by the pooled error term (e.g., $c.\beta_{US} - \Sigma V_{TOTAL\ US}$); where $c.\beta_{US}$ is the asymptote for the A-US association and $\Sigma V_{TOTAL\ US}$ represents the sum of the associative strengths of stimuli with a potential association with the US on that trial (e.g., $V_{A\text{-}US} + V_{B\text{-}US}$). We are now in a position to examine how the various associative strengths change during a true discrimination (AB+ and AC–) and a pseudo discrimination (AB+/– and AC+/–). In due course, we will also describe how reciprocal associations (e.g., A-US and US-A) and a chain of associations (e.g., A-B, B-US) are combined.



$$\Delta V_{A\text{-}US} = \alpha_A(c.\beta_{US} - \Sigma V_{TOTAL\ US}) \qquad \Delta V_{IJ} = \alpha_I(c.\alpha_J - \Sigma V_{TOTAL\ J})$$

$$\Delta V_{US\text{-}A} = \beta_{US}(c.\alpha_A - \Sigma V_{TOTAL\ A}) \qquad \Delta V_{JI} = \alpha_J(c.\alpha_I - \Sigma V_{TOTAL\ I})$$

Figure 1. Reciprocal associations (dashed lines) between the components of a compound conditioning trial (*A*, *B*, *US*), and their generalized counterparts (*I*, *J, K*); together with the (generalized) learning rules for the associations involving A and the US (and any two notional stimuli, *I* and *J*).

In the simulations, we set the learning rate parameters to .30 for A, .50 for B and C and .70 for the US; but the patterns of results are evident (if less marked) when the parameters for the stimuli (A, B and C) are equal and set to the same value as the US. To foreshadow the analysis, we will show that according to HeiDI the basis for the relative validity effect is not in the reciprocal links between the CSs (A, B and C) and the US, but rather in the links between A and B, and between A and C. We will demonstrate that the strength of these links differs between the true discrimination and the pseudo-discrimination, and these differences allow A to “borrow” less associative strength from B and C in the true discrimination than the pseudo discrimination. However, first we need to confirm that the links between the CSs and the US do not provide the basis for the relative validity effect.

Inspection of Figure 2a and 2c confirms that if we just consider the values returned for the A-US, B-US, and C-US associations, then HeiDI behaves in the same way as the Rescorla-Wagner model when β_{US} is set to the same value on reinforced and nonreinforced trials; noting that in our simulations β_{US} and c.β_{US} were simply set to 0 when the US was not presented. That is, there are differences in the associative values returned for B and C in the true discrimination, but not the pseudo discrimination, where the values returned for B and C are intermediate to those seen for these stimuli in the true discrimination. However, the associative values returned for the A-US association do not differ between the two discriminations under consideration here.

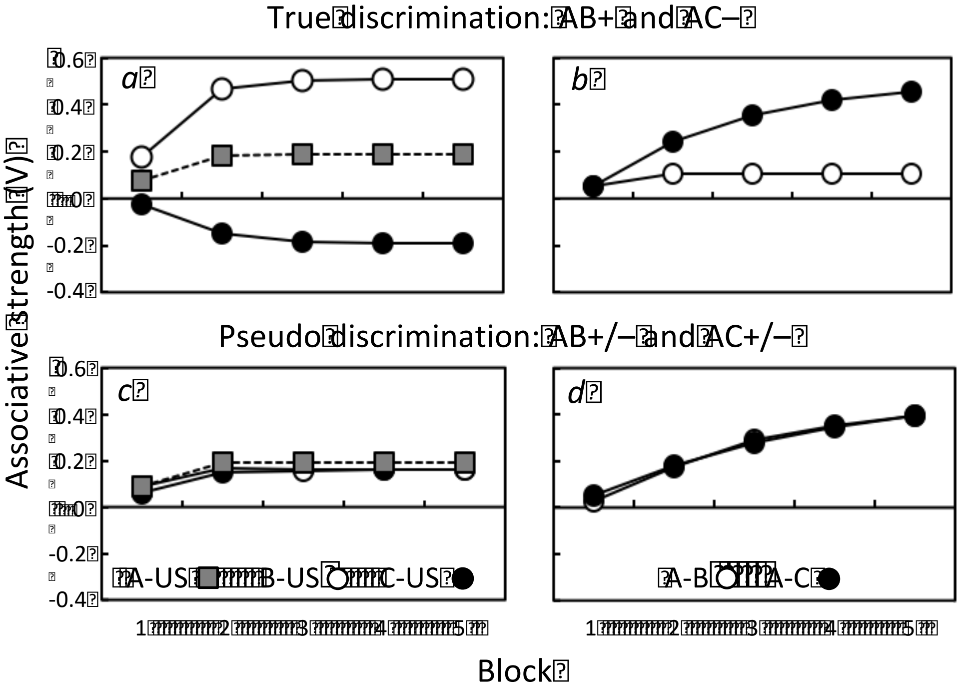


Figure 2. CS-US associations (A-US, B-US, C-US) and CS-CS associations (A-B and A-C) during the relative validity procedure. Output values for the associative strengths across 5 blocks of training for a true discrimination (AB+ and AC–; panels *a* and *b*) and a pseudo discrimination (AB+/– and AC+/–; panels *c* and *d*). The parameters used were: α_A = ..30, $\alpha_B = \alpha_C$ = .50, and β_{US} = .70 when the US is present and 0 when it is absent.

When we examine the values returned for the complementary associations (i.e., US-A, US-B, US-C) there are differences (not depicted in Figure 2). The values for the US-B and US-C associations simply reflect those seen to the corresponding forward associations; but the US-A association is stronger for the true discrimination than for the pseudo discrimination. This is because the US is presented when A is absent in the pseudo discrimination, but not the true discrimination. One way in which CS-US and US-CS associations might be combined is presented in Equation 3. According to this combination rule, V_{COMB} is equal to $V_{CS\text{-}US}$ plus the product of $V_{CS\text{-}US}$ and $V_{US\text{-}CS}$.[1] This rule recognizes the fact that while $V_{CS\text{-}US}$ is directly activated by the CS, $V_{US\text{-}CS}$ is only indirectly activated. That is, the rule has the general property that the directly activated link in a chain of associations will constrain the impact of the indirectly activated link. It is clear that when the reciprocal associations involving A and the US are combined in this way (i.e., $V_{COMB\ A\text{-}US} = V_{A\text{-}US} + (1/c.V_{A\text{-}US} \times V_{US\text{-}A})$, then HeiDI predicts that A should have a somewhat greater combined associative strength after the true than after pseudo discrimination training. That is, consideration of the associations involving the US predicts – if anything – the wrong outcome; which is supported by the results of formal simulations presented below. However, this analysis ignores the influence of the A-B and A-C associations, which provide a basis for A to "borrow" the associative properties of B and C. The values returned for these associations are depicted in Figures 2b and 2d.

$$V_{COMB} = V_{CS\text{-}US} + (\tfrac{1}{c}.V_{CS\text{-}US} \times V_{US\text{-}CS}) \quad (3)$$

Inspection of Figure 2b shows that the values returned for the A-B association for the true discrimination are smaller than those for the A-C association. This is because the US-B association restricts the growth in (i.e., overshadows) the A-B association on AB+ trials, and there is no corresponding effect on the AC– trials (cf. Holland, 1980; see also, Honey & Hall, 1992). One consequence of these differences is that A will be able to borrow relatively little of the strong excitatory properties of B, but rather more of the weak inhibitory properties of C. In contrast, inspection of Figure 2d shows that the values returned for the A-B and A-C associations are equivalently strong after a pseudo discrimination; and since B and C are both moderately excitatory, then the presentation of A will be able to borrow excitatory strength from B and C. HeiDI thereby provides a

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[1] The reciprocal of c is used to convert $V_{CS\text{-}US}$ into a dimensionless scalar.

potential analysis of the relative validity effect, once coupled with a rule for how a chain of associations (e.g., A-B, B-US) allows A to borrow associative strength from B. Equation 4 represents one such rule: The associative strength that a stimulus, A, gains indirectly through an associative chain (e.g., $V_{\text{CHAIN A-B-US}}$), involving associations from A to B ($V_{\text{A-B}}$) and B to the US ($V_{\text{COMB B-US}}$), is given by multiplying the numeric value of $V_{\text{A-B}}$ (i.e., $1/c.V_{\text{A-B}}$) by $V_{\text{COMB B-US}}$; with $V_{\text{COMB B-US}}$ being determined in the way specified in Equation 3.

The output values returned for the associative chains are depicted in panels *a* and *c* of Figure 3. Inspection of these panels confirms that for the true discrimination the values for $V_{\text{CHAIN A-B-US}}$ become positive over the 5 blocks of training, whereas those for $V_{\text{CHAIN A-C-US}}$ become negative. In contrast, the output values for both of these chains become positive across training blocks for the pseudo discrimination. The values for $V_{\text{COMB A}}$ are shown in panels *b* and *d* of Figure 3. As noted above, these values are somewhat higher for the true discrimination than the pseudo discrimination. However, when these values are combined (i.e., added) with those of the two chains (i.e., $V_{\text{COMB A + CHAINS A}}$), then the values returned are smaller for the true discrimination than the pseudo discrimination. These relatively modest numerical differences seem to contrast with the marked and (highly) consistent patterns of results observed by Wagner et al. (1968) across quite different conditioning procedures (e.g., compare the critical results from Experiment 1 (Table 2) and Experiment 3 (Table 4) in Wagner et al., 1968; see also, Cole, Barnet & Miller, 1995). However, the size of the effect predicted by our analysis would be greatly increased by assuming that the stimulus with which A has the strongest association (e.g., B or C) contributes much more to overall performance: For the true discrimination this will be C, which is a net inhibitor, whereas for the pseudo discrimination it will be either B or C, which are both excitors.

$$V_{\text{CHAIN A-B-US}} = \tfrac{1}{c}.V_{\text{A-B}} \text{ x } V_{\text{COMB B-US}} \quad (4)$$

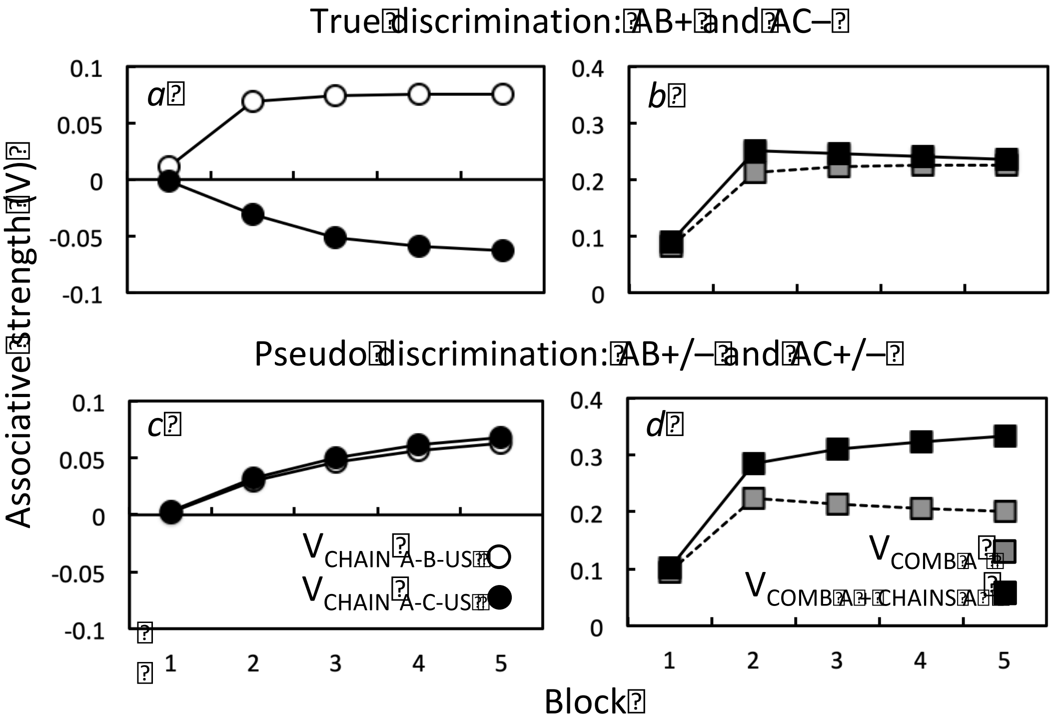

Figure 3. Output values for the associative strengths of the chains ($V_{\text{CHAIN A-B-US}}$ and $V_{\text{CHAIN A-C-US}}$), $V_{\text{COMB A}}$ and $V_{\text{COMB A}}$ plus the associative chains across 5 blocks of training. For the true discrimination (AB+ and AC–; panels *a* and *b*), and the pseudo discrimination (AB+/– and AC+/–; panels *c* and *d*) the parameters used were: $\alpha_A = .30$, $\alpha_B = \alpha_C = .50$, and $\beta_{US} = .70$ when the US is present and 0 when it is absent.

The analysis offered by the Rescorla-Wagner model for the relative validity effect required that the learning rate parameter β was higher on reinforced than nonreinforced trials. We have demonstrated that the effect can be explained without recourse to this assumption once the pooled error term operates on all of the associations that might form between stimuli on a given trial (i.e., A, B, C and the US). This analysis also provides an account for evidence that appears to provide independent support for the assumption that β is higher on reinforced than nonreinforced trials. Rescorla (2002) conducted a series of studies in which one stimulus (A) was reinforced during phase 1 and then nonreinforced in phase 2 (i.e., A+/A–) and another stimulus (B) was nonreinforced in phase 1 and then reinforced in phase 2 (i.e., B–/B+). A further two stimuli were treated in the same way during both phases: being either reinforced (C+/C+) or nonreinforced (D–/D–). All animals then received test trials with compounds AB and CD. During the test, AB elicited more responding than CD. Rescorla reasoned that this result is to be expected if the β value on reinforced B trials during phase 2 was higher than the β value for the nonreinforced A trials during phase 2. However, according to HeiDI, conditioning and extinction with A will leave the US-A association intact, and nonreinforcement followed by conditioning with B will leave B with excitatory B-US and US-B associations. In contrast, conditioning with C will mean that it has both C-US and US-C associations, but nonreinforcing D will leave it with neither. Under these conditions, AB will have stronger basis to provoke responding than CD provided it is the case that conditioning with B has proceeded until $V_{\text{COMB B-US}}$ plus $V_{\text{COMB A-US}}$ is greater than $V_{\text{COMB C-US}}$ plus $V_{\text{COMB D-US}}$.

Pooled error terms

Equations 1 and 2 use simplified forms of Equation 0 (i.e., the Rescorla-Wagner learning rule). However, there is direct evidence that appears to be inconsistent with the instantiation of the pooled error term in Equation 0 (and indeed Equation 1). Namely, if two stimuli (A and B) are paired with a US, then the associative change to each component (with the US) should be equal. In one set of experiments, Rescorla (2000) first trained two excitors (A and C), by separately pairing each with a US, and trained two inhibitors (B and D), by separately nonreinforcing each in the presence of another excitor. In a second stage, the compound AB was paired with the US, and at test the compound AD elicited less conditioned responding than BC.[2] Thus, these and other similar

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[2] The possibility that BC elicited more responding than AD because previous AB pairings enabled presentations of B to activate the excitor A (on BC test trials) and presentations of A to activate the inhibitor B (on AD test trials) was discounted on the basis of additional evidence (see Rescorla, 2000; see also, Allman & Honey, 2005).

experiments provide evidence consistent with the operation of a separate error term during compound conditioning. However, the implementation of the pooled error terms within Equations 1 and 2 from HeiDI afford an alternative analysis.

First, assume that A and C both had excitatory associative strength of .50, and B and D both had inhibitory associative strength of -.50 before the compound, AB, was paired with the US (i.e., AB+) in stage 2. According to Equations 0 and 1, the associative strength of both should increase an equivalent amount: A from .50 to .75 and B from -.50 to -.25. This would mean that the AD compound should have an associative strength of .25 (.75 + -.50) and the BC compound should also have an associative strength of .25 (.50 + -.25). However, according to HeiDI one also needs to consider the fate of the backward associations during compound conditioning: between the US and A, and between the US and B. If we assume that α for all stimuli is .30, then $V_{\text{US-A}}$ will have converged on .30 by the end of the first stage of training, but $V_{\text{US-B}}$ will be 0, because B is has not been paired with the US during this stage. This will mean that while $V_{\text{US-A}}$ will not change during pairings of AB with the US – the asymptote for $V_{\text{US-A}}$ determined by α = .30 will have been reached during the first stage of training – $V_{\text{US-B}}$ can increase (e.g., from 0 to .30). This will mean that during the test, $V_{\text{COMB BC}}$ will higher than $V_{\text{COMB AD}}$ (cf. Equation 3). This analysis shows that - even when A-B associations do not play a role – HeiDI is able to explain results taken to be inconsistent with the use of the pooled error term by the Rescorla-Wagner model (see also, Holmes, Chan, & Westbrook, 2019). The analysis is straightforward, described in greater detail in Honey et al. (2019), and can be verified using an open source app containing the code for the HeiDI model: https://ynnna.shinyapps.io/HeiDI_model/.

An associative analysis of blocking

A key feature of the Rescorla-Wagner model is that the associative strength of one stimulus (B) within a compound (AB) affects the acquisition of associative strength gained by the other stimulus (A) within that compound. For example, the model provides a simple account for blocking, where training trials in which B is paired with a US undermines the capacity of conditioning trials with AB to result in conditioned responding to A (Kamin, 1969; see Urcelay, 2017). One of the most serious challenges to the analysis of blocking provided by the model is the conditions under which "unblocking" occurs. Conventional blocking procedures involve two stages in which the reinforcer is the same: B->US and then AB->US. The fact that increasing the number of USs between stage 1 (e.g., B->US1) and stage 2 (AB->US1-US2) results in unblocking (i.e., learning about A) is perfectly consistent with the Rescorla-Wager model, because this change introduces a positive error in the pooled error term (see Equations 0 and 1). However, the fact that reducing the reinforcer (i.e., B->US1-US2 and then AB->US1) can also result in unblocking (i.e., learning about A; e.g., Dickinson, Hall, & Mackintosh, 1976) is problematic: Application of Equation 0 (and Equation 1) indicates that the reduction in the number of reinforcers will introduce a negative error in the pooled error term, which should result in A acquiring inhibitory not excitatory properties (e.g., Cotton, Goodall & Mackintosh, 1982; Nelson, 1987). *Downshift unblocking*, as it is known, has been taken as evidence that the reduction in the US prevents the reduction in attention to A that would ordinarily result from the fact that the US was fully predicted by B; and allows A to be learnt about (e.g., Mackintosh, 1975; Pearce & Hall, 1980). While there has been some progress in understanding the conditions under which downshift unblocking occurs (Holland, 1988), its explanation has remained elusive. Many have simply adopted the view that downshift unblocking is *prima facie* evidence that changes in attention play a role in blocking and other aligned phenomena (e.g., Pearce & Mackintosh, 2010); but an explanation for the effect can be derived from HeiDI, which does not appeal to changes in attention.

The essence of the analysis is that the removal of the second US (US2) during the second stage of downshift unblocking procedure allows a within-compound A-B association to form more effectively than when US2 remains; and that it is this A-B association that allows A to borrow the associative properties of B. This view receives support from results reported by Rescorla and Colwill (1983), where manipulations that should disrupt A-B associations also reduced the difference in performance to A between the standard blocking procedure and downshift unblocking. However, there has been no formal model that has implemented the interaction between such A-B associations and the associations between A and B and the US, and in particular no formal analysis of why the removal of US2 should promote a stronger A-B association. HeiDI offers one possible implementation and analysis.

Consider a blocking procedure in which B is first followed by two presentations of the same nominal US. We can treat each of the successive presentations of the US as having partially separate representations (i.e., US1 and US2). Under these conditions, B will become linked to both US1 and US2 until each link reaches the asymptote determined by $c.\beta_{US1}$ and $c.\beta_{US2}$; and critically links will be strengthened between US1 and B, and US2 and B, until their combined associative strength = $c.\alpha_B$. When AB is paired with US1 and US2, the associations between A and both US1 and US2 will be blocked; and the combined effect of the US1-B and US2-B associations will mean that A will not be able to enter association with B. However, this will not be the case when US2 is omitted. If we assume that the change in the A-B association is determined by $\alpha_A(c.\alpha_B - \Sigma V_{TOTAL\ B})$, with $\Sigma V_{TOTAL\ B} = V_{US1\text{-}B} + V_{US2\text{-}B} + V_{A\text{-}B}$, then the removal of US2 will enable the strengthening of the A-B association (and further increases in the US1-B association). Under these conditions, downshift unblocking will occur to the extent that the influence of the A-B association in retrieving the associative properties of B (stronger following downshift unblocking than standard blocking) outweighs the fact that the B-US2 (is weaker) and A-US2 (is negative) after downshift unblocking. This analysis is formally presented in Honey et al. (2019), and can also be verified using the open source HeiDI app.

Finally, studies reported by Pearce and colleagues have demonstrated an effect, dubbed *the redundancy effect*, which appears to be beyond the scope of error-correcting rules of the type used in a variety of formal models of Pavlovian learning including HeiDI. They showed that when A was trained as part of a blocking procedure (B+/AB+) it elicited more responding than when it was trained as part of a true discrimination (AB+/AC–; see this issue, Uengoer, Lachnit, & Pearce, 2019; see also, for example, Jones & Pearce, 2015; Pearce, Dopson, Haselgrove & Esber, 2012). This is a surprising finding, because A should have gained a weaker association with the US as a consequence of the blocking procedure than the true discrimination. But, could within-compound associations (e.g., A-B and A-C) play a role? We have already seen that the net associative strength that A could borrow from B and C after a true discrimination is negligible, but the ability of A to borrow from B after a blocking treatment will also be negligible to the extent that the A-B association is subject to blocking by the US-B association; remembering that HeiDI is implemented as a trial-based model. In fact, the issue around whether differences in such within-compound associations might generate the redundancy effect is moot: Pearce et al. (2012; see also, Uengoer, Lotz, & Pearce, 2013) showed that the critical differences in responding to A survived post-training procedures designed to reduce the associative strength of B (for the blocking condition) and increase the associative strength of C (for the true discrimination condition): A continued to elicit significantly more responding in the blocking condition than in the true discrimination condition.

Rather than reject models based on this observation, perhaps one should consider a simpler explanation. It seems plausible to argue that during a redundancy procedure, the response elicited by B will be better able to support the development of a Stimulus-Response association – an A-R association – in the blocking condition than will the responses elicited on separate trials by B and C in the true discrimination condition. To be clear, this form of explanation does not appeal to any form of higher-order conditioning involving the formation of a link between the representations of A and B (or A and C), just changes in the links from the representation of one stimulus (A) to the response-generating processes activated by other stimuli that co-occur with A (i.e., B and C). An analogous form of explanation could also be applied to the relative validity effect. Clearly, further work is needed to understand the origin of the redundancy effect, and we will return to the role of Stimulus-Response links in generating conditioned responding when we describe the performance rules for HeiDI.

An associative analysis of latent inhibition

Rescorla and Wagner (1972) recognized the fact that their model did not immediately address the observation that preexposure to a CS retards later excitatory and inhibitory conditioning (for a review, see Hall, 1991; Lubow, 1989). That is, the original model did not provide an account of latent inhibition (Lubow & Moore, 1959). Why should repeated presentation of a to-be-conditioned stimulus affect the rate at which (excitatory and inhibitory) conditioned performance emerges to that stimulus? This observation, like downshift unblocking, prompted some theorists to conclude that models of Pavlovian conditioning needed to include another process that changes as a function of experience: attention, associability or CS processing (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Wagner, 1981). Perhaps this conclusion too was premature.

Latent inhibition is context specific. If preexposure to the CS occurs in one context (defined by the cues present in one experimental chamber) and conditioning takes place in another context, then latent inhibition is much reduced (e.g., Hall & Honey, 1989; Honey & Good, 1993; Lovibond, Preston, & Mackintosh, 1984). The general significance of this observation is that it suggests that animals learn about the context in which the stimulus has been presented: They form a context-CS association (cf. Wagner, 1981). This observation enables HeiDI to provide a simple analysis of latent inhibition: the blocking of the US-CS association by the context-CS association. We have argued that during excitatory conditioning, performance is determined by both a CS-US association and a US-CS association; and we assume that during inhibitory conditioning, performance reflects the status of both a CS-No US and a No US-CS association (Konorski, 1967). While a context-CS association will not block the CS-US and CS-No US associations, it will block the development of the US-CS and No US-CS associations. Thus, the simple inclusion of a US-CS association (and No US-CS association) enables an account of latent inhibition that does not require a separate attentional or associability process (e.g., Mackintosh, 1975; Pearce & Hall, 1980) or changes in CS processing of the form envisaged by Wagner (1981; see also McLaren & Mackintosh, 2000).

HeiDI: Performance rules

HeiDI provides an analysis for phenomena that are beyond the scope of the Rescorla-Wagner model, largely because it appeals to reciprocal associations, the formation of which is governed by (simplified) learning rules with pooled error terms. In the context of Pavlovian conditioning, the reciprocal associations involve the CS and the US, and the combined value of these associations is given by Equation 3 and can be borrowed by stimuli associated with the CS in the way specified in Equation 4. It is now time to consider how associative knowledge maps onto conditioned behavior.

The assumption made by the Rescorla-Wagner model, together with a succession of other influential models, was an acknowledged simplification: "*For the analyses we wish to present in this paper, it will generally be sufficient simply to assume that the mapping of Vs into magnitude or probability of conditioned responding preserves their ordering.*" (p. 77, Rescorla & Wagner, 1972). Recent evidence confirms the inadequacy both of this assumption and the idea that Pavlovian conditioning results in unconditioned responses snipped from the US being grafted onto the CS (see Warner, 1932; see Pavlov, 1927; see also, Dwyer, Burgess, & Honey, 2012; Wagner & Brandon, 1989). For example, studies of autoshaping in rats in which the brief insertion of a lever (the CS) is immediately followed by the delivery of an appetitive US (e.g., sucrose or a food pellet) into a recessed food well produces marked individual differences in behavior: Some rats express what they have learnt by interacting with the lever, others by investigating the location where the reinforcer is about to be delivered, with the remaining rats showing patterns of behavior in between these two extremes (e.g., Iliescu et al., 2018; Flagel et al., 2009, 2011; Patitucci et al., 2016; see also, Matzel et al., 2003). Activity directed towards the lever is often called sign-tracking (e.g., Hearst & Jenkins, 1974; see also, Davey & Cleland, 1982; Timberlake, Wahl, & King, 1982) and activity directed towards the food well is called goal-tracking (e.g., Boakes, 1977; Delamater, 1995; Good & Honey, 1991).

The results from an illustrative study are shown in Figure 4 (Patitucci et al., 2016). In this study, the insertion of one lever was followed by sucrose and the insertion of another (control lever) was not. A median split was used to separate rats into two groups (called sign-trackers and goal-trackers) on the basis of whether their activity during the final block of training (block 6) was predominantly directed towards the lever or food well, which allows the development of the sign-tracking and goal-tracking phenotypes to be traced across training. However, analysis at the level of individual rats reveals that the bias towards sign-tracking or goal-tracking is relatively continuous in nature across a group of rats. The upper panels of Figure 4 show the development of lever activity to the lever paired with sucrose and to the control lever followed by no sucrose in the sign-tracking rats (left panel) and goal-tracking rats (right panel). The lower panels show the levels of food well activity across training. When lever activity is used as the assay of discrimination learning, the sign-tracking group show better learning than the goal-tracking group; but when food well activity is used then the reverse is the case. That is, it is not possible to provide a mapping of Vs on to conditioned behavior that provides a coherent interpretation: Focusing on sign-tracking, for example, leads to the conclusion that associative learning had proceeded more readily in one set of rats than the other, while focusing on goal-tracking leads to the opposite conclusion. In general, the Rescorla-Wagner model cannot explain why, for any given rat, one response was stronger than the other, and why in some rats goal-tracking was stronger than sign-tracking whereas in other rats the opposite was the case. Indeed, these results pose and equivalent problem for any theory of learning that assumes a monotonic relationship between a single construct that represents learning and acquired behavior (e.g., Gallistel & Gibbon, 2000; Stout & Miller, 2007).

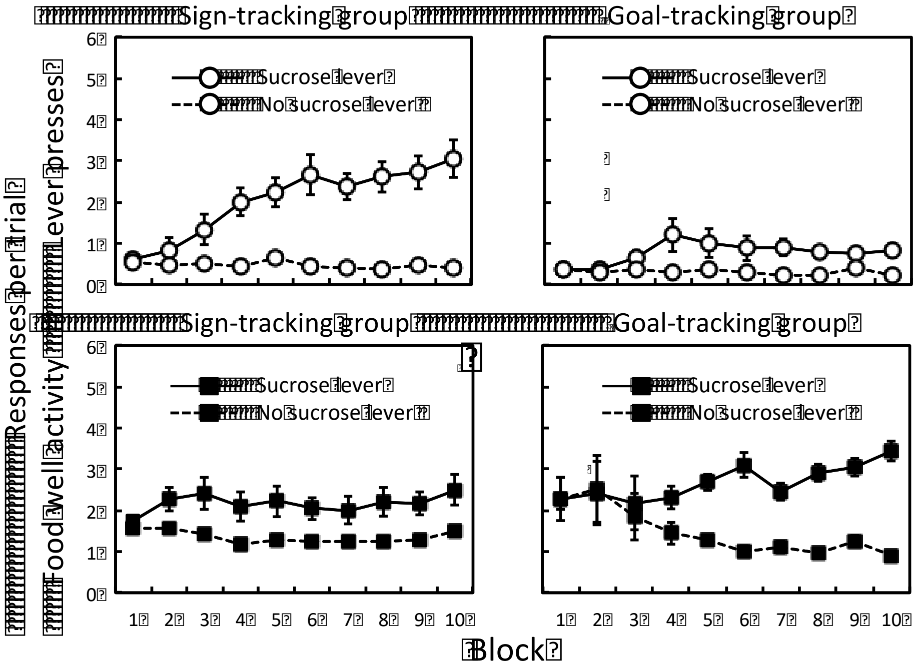
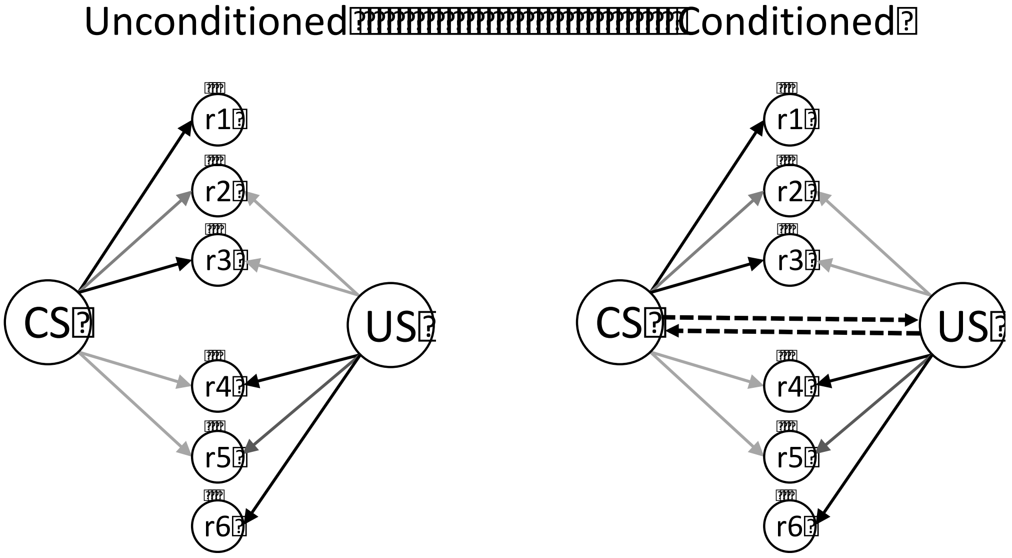


Figure 4. *Differences in the form of conditioned behavior*. Mean (± SEM) levels of lever activity (sign-tracking) and food well activity (goal-tracking) across 10 training blocks. Rats were divided into sign-trackers (left panels) and goal-trackers (right panels), and the scores are separated for the lever paired with sucrose and the lever that was not. Adapted from: Patitucci, E., Nelson, N., Dwyer, D.M., & Honey, R.C. (2016). The origins of individual differences in how learning is expressed in rats: A general-process perspective. *Journal of Experimental Psychology*: *Animal Learning and Cognition, 42,* 313-324.

Figure 5 provides a schematic for the associative structures to which we will align our analysis of how learning affects behavior in Pavlovian conditioning. We adopt a general distinction between unconditioned responses that are mainly based on the properties of the CS (r1-r3) and those that are mainly based on the properties of the US (r4-6; see Holland, 1977, 1984). Before conditioning has taken placed, the CS is strongly linked to a set of unconditioned responses (r1-r3; e.g., orienting, lever approach, rearing), whereas the US is strongly linked to a set of unconditioned responses (r4-r6; e.g., food well approach, chewing, swallowing). The links from the CS to r4-r6 and from the US to r1-r3 are assumed to be very weak; with the weights of the lines between the CS and r1-r6 and between US and r1-r6 denoting the relative strengths of these untrained or unconditioned links.[3] The reciprocal CS-US and US-CS associations are depicted as the presence of dashed lines in the conditioned structure. Importantly, while the development of the CS-US association increases the likelihood that the presentation of the CS will activate the US and thereby provoke r4-r6, without the backward associations there would be little change in the likelihood that the CS would provoke r1-r3. The CS-US association allows the presentation of the CS to activate the US representation and US-CS association allows activation of the US to activate the CS representation, which increases the tendency for r1-r3 to become active as a consequence of conditioning.


Unconditioned

Conditioned

Figure 5. Schematic associative structures that underpin the translation of (excitatory) learning into performance. The left-hand depicts the unconditioned structure (i.e., before conditioning), with the darkness of the links between the CS and r1-r6 and the US and r1-r6 indicating their strength, and the right-hand side depicts the conditioned structure (i.e., after conditioning). The reciprocal CS-US and US-CS associations are denoted by the dashed lines. Adapted from: Honey, R.C., Dwyer, D.M., & Iliescu, A.F. (2019). HeiDI: A model for Pavlovian learning and performance with reciprocal associations. *Psychological Review* (under review).

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[3] In the interests of simplicity, we have assumed that these unconditioned links have strengths that are fixed; but we should also acknowledge the possibility that they might change as the result of experience and thereby provide a potential basis for S-R learning (cf. Pearce et al., 2012; Uengoer et al., 2013).

One way to distribute the combined strength of the reciprocal associations (i.e., V_{COMB}) into components that support different classes of behavior, CS-oriented (e.g., sign-tracking) and US-oriented (e.g., goal-tracking), is according to the relative perceived saliences of the CS and US (i.e., α_{CS} and β_{US}). The inadequacy of this proposal is clear: While the perceived salience of a CS will be directly given when it is presented, that of the US will not. For this reason, we propose that the distribution of V_{COMB} is determined by the value of α_{CS} relative to $V_{CS\text{-}US}$ (which reflects β_{US}). That is, the perceived salience of the CS (α_{CS}) relative to its capacity to activate the US representation (i.e., $V_{CS\text{-}US}$). Equations 5 and 6 make that relationship transparent and generate two values, R_{CS} and R_{US}, which influence the levels of CS-oriented and US-oriented responding, respectively. According to these equations, R_{CS} will dominate R_{US} when $\alpha_{CS} > V_{CS\text{-}US}$, but the reverse will be the case when $V_{CS\text{-}US} > \alpha_{CS}$. To address the fact that Equation 1 (and Equation 2) can return negative Vs, the use of absolute values in Equations 5 and 6 ensures that the proportions are ≤ 1. As before, $|V_{CS\text{-}US}|$ is transformed into a dimensionless value by multiplying it by 1/c, which means that R_{CS} and R_{US} are in units of V.

$$R_{CS} = \frac{\alpha_{CS}}{\alpha_{CS} + \frac{1}{c}.|V_{CS\text{-}US}|} V_{COMB} \qquad (5)$$

$$R_{US} = \frac{\frac{1}{c}.|V_{CS\text{-}US}|}{\alpha_{CS} + \frac{1}{c}.|V_{CS\text{-}US}|} V_{COMB} \qquad (6)$$

It is worth highlighting the fact that while Equations 1 and 2 embody the idea that the perceived salience of stimuli (e.g., CS and US) influences learning, Equations 5 and 6 capture the idea that their perceived salience affect the expression of learning: the CS directly and the US through $V_{CS\text{-}US}$. In the case of Pavlovian conditioning, the two rules governing the distribution of V_{COMB} into R_{CS} and R_{US} have the general properties that when $V_{CS\text{-}US}$ is low, then R_{CS} will be greater and CS-oriented responding becomes more likely (via r1-r3 in Figure 5); and that as $V_{CS\text{-}US}$ grows, R_{US} becomes greater and US-oriented responding becomes more likely (via r4-r6 in Figure 5; cf. Kaye & Pearce, 1984). Equations 5 and 6 are readily extended to accommodate stimulus compounds (e.g., AB). To do so, the α values for A and B are simply combined (e.g., added) to form α_{AB}, and the net Vs of A and B are combined (e.g., added) to form $V_{AB\text{-}US}$. Similarly, a given stimulus (CS or US) can be conceived of as a set of elements with their own α values and net Vs, which could be entered into Equations 5 and 6 using the same approach (cf. Atkinson & Estes, 1963; see also, Delamater, 2012; Wagner & Brandon, 1989). The simulations shown in Figure 6 illustrate how R_{CS} and R_{US} change as a function of variations in the perceived salience of the CS and US.

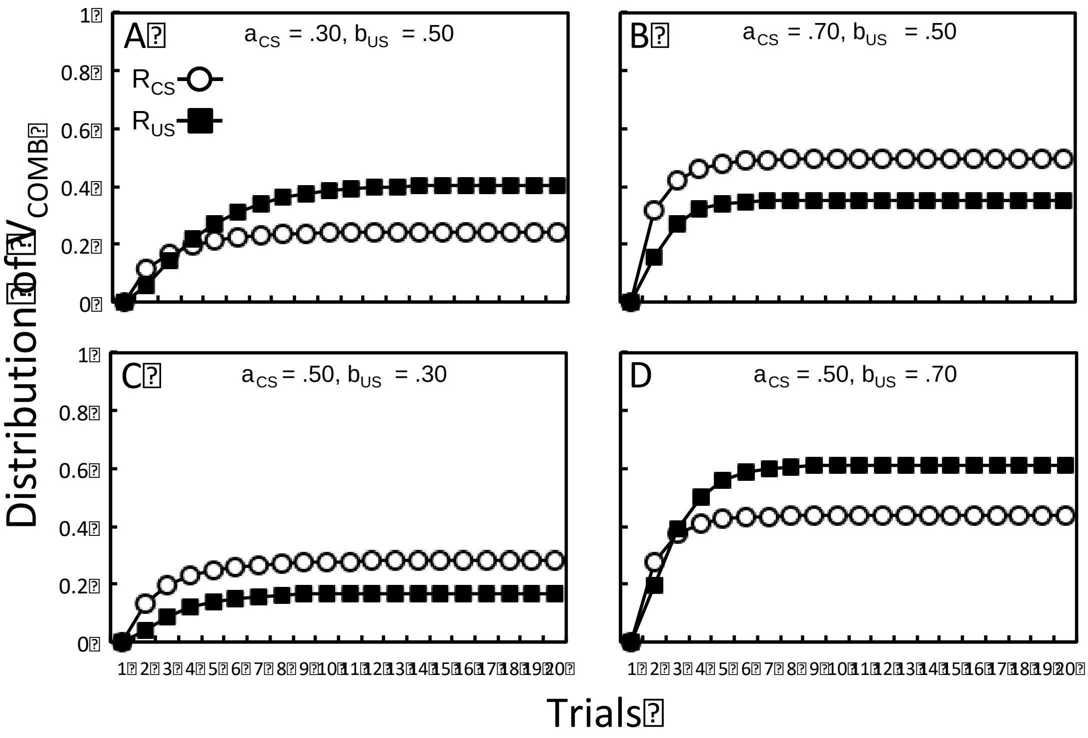

Figure 6. Simulations of the distribution of V_{COMB} into R_{CS} and R_{US} across 20 conditioning trials. R_{CS} and R_{US} outputs were generated using the values for V_{COMB} taken from the same combinations of α_{CS} and β_{US} that were entered into Equations 5 and 6. In panels A and B, α_{CS} was either .30 (A) or .70 (B) and β_{US} was fixed at .50; and in panels C and D, α_{CS} was fixed at .50 and β_{US} was either .30 (C) or .70 (D). Adapted from: Honey, R.C., Dwyer, D.M., & Iliescu, A.F. (2019). HeiDI: A model for Pavlovian learning and performance with reciprocal associations. *Psychological Review* (under review).

Equations 5 and 6 provide a simple basis for the combined associative properties of a given pair of stimuli (i.e., V_{COMB}) to be distributed into two components (R_{CS} and R_{US}) that are held to affect one subset of response units (r1-r3) more than another (r4-r6). However, these equations do not specify how individual response units become active. One simple possibility is expressed in Equation 7, where the activation of a given response unit (e.g., r1) is simply determined by adding the products of: (i) multiplying the translated value of R_{CS} by the unconditioned link between the CS and r1 (i.e., $V_{CS\text{-}r1}$), and (ii) multiplying the translated R_{US} value by the strength of connection between the US and the same response unit (i.e., $V_{US\text{-}r1}$). Again, R_{CS} and R_{US} are translated into dimensionless values through multiplication by the reciprocal of the constant, c. We can then assume that the product of Equation 7 (e.g., r1, which is in units of V) is reflected in the overt response (i.e., $r1_{overt}$). There are more complex ways in which R_{CS} and R_{US} might affect r1-r6, involving the interaction between the products of Equation 7 across the set of response-generating units (r1-r6; e.g., McClelland & Rumelhart, 1981); or perhaps through a process of peripheral interference between the outputs of response units (i.e., response competition). These changes would result in more marked divergence between different responses than would be arise from Equation 7 alone, and the corresponding R_{CS} and R_{US} values in Figure 6.

$$r1 = \left(\tfrac{1}{c}.R_{CS} \times V_{CS\text{-}r1}\right) + \left(\tfrac{1}{c}.R_{US} \times V_{US\text{-}r1}\right) \quad (7)$$

To summarize: According to the analysis outlined above, individual differences in the nature of conditioned responding reflect the perceived intensities of the CS (directly) and the US (less directly), which affect performance via unconditioned links between the CS, US and response-generating units (r1-r6 in Figure 5). However, another potential basis for individual differences is in the initial strengths of these unconditioned links, which we could further suppose change as a result of experience. We have already appealed to changes in such links to explain (features of) the redundancy effect.

HeiDI: Preliminary evidence

We assume that α_{CS} and β_{US} are fixed in a given animal for a given CS and US, but propose that the perceived salience of the CS (relating to α_{CS}) and US (relating to β_{US}), and hence α_{CS} and $V_{CS\text{-}US}$ in Equations 5 and 6, can vary between animals. This proposition provides the basis for individual differences in R_{CS} and R_{US}, because α_{CS} and $V_{CS\text{-}US}$ affect performance according to Equations 5 and 6.[4] This analysis is supported by the observation that rodents who showed a strong liking for sucrose (as measured by licking microstructure; see Dwyer, 2012) are more likely to be goal-trackers (when sucrose was the US) than those who exhibited a weaker liking for sucrose (Patitucci et al., 2016; see also, Morrison et al., 2015). Individual variation in the palatability of sucrose can be aligned to differences in β_{US} that will affect both learning (i.e., the asymptotic value of $V_{CS\text{-}US}$ and the rate at which $V_{US\text{-}CS}$ reaches asymptote, through Equations 1 and 2) and the distribution of V_{COMB} in performance (through $V_{CS\text{-}US}$ in Equations 5 and 6). Indeed, Dwyer, Figueroa, Gasalla, and Lopez (2018) showed that individual differences in the palatability of sucrose (during their experiments involving contrast effects) were positively correlated with flavor preference learning. The proposition that β_{US} for different USs varies between and within animals is also supported by two observations: When separate presentations of two levers are paired with the same US (e.g., food or sucrose) then the bias towards sign-tracking or goal-tracking on one lever correlates with the bias on the other (Iliescu et al., 2018); but, when the presentation of one lever is paired with sucrose and the other lever is paired with food there is no correlation between the bias on the two levers (Patitucci et al., 2016). This

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[4] Equations 5 and 6 can be transformed for the case in which the US is presented alone: Under these conditions, β_{US} replaces α_{CS} and $1/c.|V_{US\text{-}CS}|$ replaces $1/c.|V_{CS\text{-}US}|$.

pattern of results is consistent with the view that the β_{US} values for two USs (i.e., food and sucrose) can vary between animals and within a given animal (cf. Rescorla & Wagner, 1972).

A central prediction of HeiDI is that variation in $1/c.|V_{CS\text{-}US}|$ interacts with α_{CS} in determining performance (see Equations 5 and 6). This prediction receives support from the different effects of an extinction procedure on sign-tracking and goal-tracking. According to HeiDI, extinction trials should results in a reduction in net $V_{CS\text{-}US}$, conditional on the reduction of β_{US} from a positive value to 0 in Equation 1. This will mean that V_{COMB} declines (see Equation 3), which will affect a reduction in both R_{CS} and R_{US} (according to Equations 5 and 6). However, Equations 5 and 6 also predict that this decrease will be less marked for R_{CS} than for R_{US}: because while α_{CS} will remain the same during extinction, $1/c.|V_{CS\text{-}US}|$ will be lower. This will increase the proportion of V_{COMB} that is distributed to R_{CS} relative to R_{US}. This prediction was confirmed in groups of rats that were designated as either sign-trackers or goal-trackers (Ilescu et al., 2018): In both groups, sign-tracking declined less rapidly during extinction than did goal-tracking.

The results from a related conditioning preparation provide converging evidence for the proposed interaction between α_{CS} and $V_{CS\text{-}US}$ in determining R_{CS} and R_{US}. Kaye and Pearce (1984) gave rats trials on which presentations of a localized light were either paired with the delivery of a food pellet on every trial (continuous reinforcement) or on a randomly scheduled 50% of trials (partial reinforcement). Continuous reinforcement maintained a higher level of goal-tracking (entering the food well) and a lower level of sign-tracking (orienting and approaching the light) than did partial reinforcement (see also, Anselme, Robinson, & Berridge, 2012). According to Equation 1, $V_{CS\text{-}US}$ will be higher during continuous than partial reinforcement, and given the fact that α_{CS} does not depend on the reinforcement schedule then Equations 5 and 6 will return higher values for R_{US} and lower values for R_{CS} during continuous reinforcement than during partial reinforcement. These values should be reflected in more US-oriented responses than CS-oriented responses during continuous than partial reinforcement (Equation 7). Moreover, the fact that CS-oriented behavior is less well maintained by continuous than by partial reinforcement could also interfere with an animal's later ability to detect new relationships involving a continuously reinforced CS (cf. Pearce & Hall, 1980; Pearce, Wilson, & Kaye, 1988; Swan & Pearce, 1988; Wilson, Boumphrey, & Pearce, 1992; see also, Meyer, Cogan, & Robinson, 2014; Nasser, Chen, Fiscella, & Calu, 2015; Robinson & Flagel, 2009). This analysis rests on the plausible assumption that low levels of orienting to a CS could affect its reception and concomitant association with another stimulus.

General Discussion

The theoretical contributions of Allan R. Wagner have shaped the field of animal learning theory, and beyond. The model that he proposed, with his colleague Robert A. Rescorla, has an enduring influence: The theory is the benchmark against which new results and theoretical innovations are judged. His later theoretical contributions were ambitious, but were united by a desire to explain complex phenomena in terms of a limited set of core principles: They involved pursuing real-time (rather than trial-based) analyses of conditioning phenomena, including the differing temporal dynamics of the representations of the CS and US (SOP, Wagner, 1981; ÆSOP, Wagner & Brandon, 1989); and re-casting the nature of the representations that entered into associations (e.g., Brandon, Vogel, & Wagner, 2000; Wagner, 2003). How combining one stimulus with another stimulus affects their functional properties remains an ongoing issue for future research.

As we have already noted, there has been little appetite to understand individual differences in the strength and nature of conditioned responses. For example, when comparing conditioning involving a single CS with conditioning involving a compound of two CSs, Wagner and Rescorla (1972; pp. 303-304) noted "*that the greater the number of cues which is made available, the more likely it is that the subject will be provided (and perhaps idiosyncratically so) with a single salient cue to which conditioning can rapidly occur*." Animals might exhibit idiosyncratic differences in the rates of conditioning to different stimuli (see also, Pavlov, 1941, pp. 373-378), but these differences have been of little interest to theorists attempting to elucidate general principles of learning (see also, for example, Mackintosh, 1975; Miller & Matzel, 1988; Pearce, 1994; Pearce & Hall, 1980, Stout & Miller, 2007; but see, Lesaint, Sigaud, Flagel, Robinson, & Khamassi, 2014).

HeiDI is an attempt to develop a general process, trial-based model of associative learning that also addresses individual differences in the strength and form of conditioned behavior. This enterprise seemed to us both timely and worthwhile. For example, individual differences in conditioned behavior can be more marked than the type of group-level differences that have motivated the development of associative theory over the past 50 years (see Figure 3). The model that we have developed is based on the Rescorla-Wagner model, but it takes their trial-based analysis and applies it to the (reciprocal) associations between all of the stimuli presented on a given trial. This approach allows HeiDI to provide an account for a broad range of phenomena, which either required the Rescorla-Wagner model to make somewhat arbitrary assumptions (e.g., Wagner et al., 1968), or were inconsistent with the instantiation of the pooled error term that they first described (e.g., Dickinson et al., 1976; Rescorla, 2000).

The analysis of how individual differences in performance emerge from differences in the perceived salience of the CS and US is simple, but it might seem implausible: Even if there were differences in the perceived salience of a CS or US across different animals, could these be sufficiently marked that a CS would be perceived as more salient than a US? Perhaps not. However, conditioning procedures have been titrated in such a way that CSs will provoke conditioned behaviors when paired with USs: Rats are sufficiently hungry that a measureable behavioral response occurs to the insertion of a lever that precedes the delivery of a food pellet in an otherwise bare chamber. Perhaps these are precisely the conditions under which relatively small variations in the perceived salience of a CS or US would play a significant role. This form of analysis could be assessed by systematically varying (e.g., reducing) the food restriction schedule used to maintain animals and examine how this changes (e.g., reduces) the biases towards goal-tracking and sign-tracking. Irrespective of arguments around the plausibility of our analysis, there is evidence that is consistent with it (e.g., Ilescu et al., 2018; Patitucci et al., 2016). If individual differences in the perceived salience of the CS and US do play a role in the form of conditioned behavior, then the next step is to isolate the origin of these differences.

To conclude: Two central issues need to be evaluated in order to determine the merit of the novel analysis of individual and group-level differences in conditioned behavior offered by HeiDI. First, the perceived saliences of both the CS and US need to be evaluated prior to conditioning, in order to examine whether they predict individual differences in the strength and form of conditioned behavior. Second, the strengths of the various within-trial associations, which are the basis of the analysis offered for various group-level effects, need to be determined. Securing this evidence will enable business left unfinished by HeiDI’s academic grandfather to be addressed, and new avenues to be explored. We too think that this enterprise has the potential to provide fundamental insights into learning and behavior more broadly.

List of equations

0. $DV_{\text{CS-US}} = a_{\text{CS}}.b_{\text{US}}(\lambda - \Sigma V_{\text{TOTAL-US}})$

1. $DV_{\text{CS-US}} = a_{\text{CS}}(c.b_{\text{US}} - \Sigma V_{\text{TOTAL-US}})$

2. $DV_{\text{US-CS}} = b_{\text{US}}(c.a_{\text{CS}} - \Sigma V_{\text{TOTAL-CS}})$

3. $V_{\textbf{COMB}} = V_{\textbf{CS-US}} + (\frac{1}{c}.V_{\textbf{CS-US}} \text{ x } V_{\textbf{US-CS}})$

4. $V_{\textbf{CHAIN A-B-US}} = \frac{1}{c}.V_{\textbf{A-B}} \text{ x } V_{\textbf{COMB B-US}}$

5. $R_{\text{CS}} = \frac{\mathbf{a_{CS}}}{\mathbf{a_{CS}} + \frac{1}{c}.|\mathbf{V_{CS\text{-}US}}|} V_{\text{COMB}}$

6. $R_{\text{US}} = \frac{\frac{1}{c}.|\mathbf{V_{CS\text{-}US}}|}{\mathbf{a_{CS}} + \frac{1}{c}.|\mathbf{V_{CS\text{-}US}}|} V_{\text{COMB}}$

7. $r1 = \left(\frac{1}{c}.R_{\text{CS}} \times \Delta V_{\text{CS-r1}}\right) + \left(\frac{1}{c}.R_{\text{US}} \times \Delta V_{\text{US-r1}}\right)$

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