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Evidence for multiple processes contributing to the Perruchet effect: Response priming and associative learning.

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Abstract

The Perruchet effect constitutes a robust demonstration that it is possible to dissociate conditioned responding and expectancy in a random partial reinforcement design across a variety of human associative learning paradigms. This dissociation has been interpreted as providing evidence for multiple processes supporting learning, with expectancy driven by cognitive processes that lead to a Gambler's fallacy, and the pattern of conditioned responding (CRs) the result of an associative learning process. An alternative explanation is that the pattern of CRs is the result of exposure to the unconditioned stimulus (US). In three human eyeblink conditioning experiments we examined these competing explanations of the Perruchet effect by employing a differential conditioning design and varying the degree to which the two conditioned stimuli (CS) were discriminable. Across all of these experiments there was evidence for a component of the CRs being strongly influenced by recent reinforcement, in a way that was not demonstrably influenced by manipulations of CS discriminability, which suggests a response priming mechanism contributes to the Perruchet effect. However, the complete pattern of results and an analysis of the results from previously published studies are also consistent with there being an associative contribution to the effect.

Evidence for multiple processes contributing to the Perruchet effect: Response priming and associative learning.

Associative learning is the ability, which is thought to be almost ubiquitous in the animal kingdom, to learn about stimuli or events that co-occur closely in time and space. For example, in Pavlovian conditioning pairing an initially neutral conditioned stimulus (CS e.g. a tone) with a biologically significant unconditioned stimulus (US e.g. a puff of air to the eye) results in the acquisition of a conditioned response (CR) to the CS (e.g. a blink to the tone in anticipation of the puff of air). Humans can also indicate when they have learned this association by describing the nature of the contingency between the CS and the US or by merely indicating when they expect the US to occur.

It has been suggested that there are two separate learning processes in operation during human associative learning, including Pavlovian conditioning (McLaren et al., 2014; McLaren, Green, & Mackintosh, 1994). The first process involves the formation of a link between the mental representations of the CS and the US such that CS presentation activates the US representation to produce the CR. The mental representation can be as simple as the activation of a specific unit or collection of neurons, and the formation of the association is a result of the co-activation of the mental representations. The second process involves the induction or application of rules or propositions within the cognitive system that can be applied flexibly and modified by instruction. While this dual-process view of learning is widely accepted, empirical reviews of the literature have revealed relatively few instances in which a clear dissociation between these two hypothesized systems has been unequivocally demonstrated (Lovibond & Shanks, 2002).

To date, the most convincing evidence in favor of a dual-process view of associative learning is the Perruchet effect (Perruchet, 1985). The Perruchet effect entails a concurrent dissociation between participants' expectancy for an outcome and the related behavioral response under conditions of partial reinforcement or intermittent pairing. This concurrent dissociation has been reliably demonstrated in human eyeblink conditioning (Perruchet, 1985; Weidemann, Broderick, Lovibond, & Mitchell, 2012; Weidemann, Tangen, Lovibond, & Mitchell, 2009), a cued reaction time task (Barrett & Livesey, 2010; Livesey & Costa, 2014; Mitchell, Wardle, Lovibond, Weidemann, & Chang, 2010; Perruchet, Cleeremans, & Destrebecqz, 2006), in human electrodermal conditioning (McAndrew, Jones, McLaren, & McLaren, 2012; McAndrew, Weidemann, & McLaren, 2013; Perruchet, Grégoire, Aerts, & Poulin-Charronnat, 2015), and in other associative learning paradigms (Jiménez & Méndez, 2013; Moore, Middleton, Haggard, & Fletcher, 2012; Moratti & Keil, 2009).

In the eyeblink Perruchet Effect, participants are exposed to a procedure in which a tone is followed by an airpuff to the eye, half of the time, and presented on its own, half of the time. There is a 50% chance of the next trial being a tone-airpuff trial and a 50% chance of it being a tone-alone trial, regardless of what happened on the previous trial except after four consecutive trials because after this the sequence was artificially truncated. In Perruchet's (1985) original demonstration, participants made expectancy ratings in the intertrial interval for the airpuff following the next tone. When responding was assessed according to the type of trial or trials immediately preceding the current trial, Perruchet found that expectancy for the airpuff decreased following a series of consecutive tone-airpuff trials, and increased following a series of consecutive tone-alone trials. That is, participants showed the common gambler's fallacy for when they expected the airpuff to occur (Burns & Corpus, 2004; Keren & Lewis, 1994). Importantly, participants' eyeblink CR to the tone revealed the opposite pattern: as the number of consecutive tone-airpuff trials increased, participants' eyeblink CRs increased and as the number of consecutive tone-alone trials increased participants' eyeblink CRs decreased.

However, for the Perruchet effect to represent evidence of two distinct learning processes, the changes in expectancy and the behavioral response must each reflect *learned* changes. That is, changes in expectancy must reflect changes in cognitive beliefs, and changes in behavior must reflect changes in the strength of an associative link. An alternative explanation for the changes in behavior is that they may be a consequence of presenting the outcome stimulus. In the case of the eyeblink Perruchet effect, the increases in CRs following tone-airpuff trials may be the result of having recently received an airpuff and the decrease in eyeblink CRs following tone-alone trials may be the result of not having received an airpuff recently. If the changes in eyeblink CRs in the Perruchet effect are the result of changes in responding due to the US then the dissociation may not constitute evidence for the two learning processes originally supposed.

Perruchet (1985) recognized that the changes in eyeblink CRs may be the result of the US and so conducted a second experiment to test this possibility. This experiment included a control group where the tone and the airpuff were explicitly unpaired and participants were presented with airpuff-alone and tone-alone trials in place of the tone-airpuff and tone-alone trials in the experimental group. The standard upward linear trend in eyeblink CRs was seen in the experimental group but was absent in the control group, although there was more responding following airpuff-alone trials than tone-alone trials. Subsequently Weidemann et al. (2009) tested two additional variants of Perruchet's (1985) control condition in which occasional runs of airpuff-alone and blank trials were interspersed among tone-alone and tone-airpuff trials. In both of these experiments there was evidence for the standard upward linear trend in eyeblink CRs following runs of tone-alone and tone-airpuff trials, but this linear trend was absent following runs of airpuff-alone and blank trials. Together these results suggest that the changes in eyeblink CRs in the Perruchet effect are the result of associative processes.

However, each of these control groups is potentially compromised in its ability to detect response priming of eyeblink CRs by the US. In Perruchet's (1985) control group the tone and the airpuff were explicitly unpaired, consequently the effect of the US on responding to the CS may have been obscured by the lack of any associative connection between the CS and the US. If the strength of the CS-US association was weak then priming the response, by presenting the US, may not have had any effect on responding to the CS because there is no response to the CS to be primed. However in the standard Perruchet condition the CS produces a CR that might be primed by the US presentation. Thus the unpaired control group is not the most appropriate test of response priming. In Weidemann et al.'s (2009) control groups there was a CR that could be primed but there were relatively few instances where response priming independent of any associative contribution could be assessed. This is because response priming could only be assessed when the CS was presented following a run of US-alone and blank trials. Also, there were many fewer US-alone and blank trials than CS-US and CS-alone trials. This relative paucity of trials on which to assess responding, and the inherent variability in the conditioned eyeblink response may have led to a lack of power in assessing response priming by the US.

In the reaction time (RT) version of the Perruchet effect there is evidence of a response priming contribution, that is, the recent performance of the response facilitates subsequent response performance. In the RT Perruchet effect participants are presented with a tone on every trial and on 50% of trials this is followed by a square which participants are required to respond to with a button press as quickly as possible (Perruchet, Destrebecqz, & Cleeremans, 2006). In a series of three experiments, Mitchell et al. (2010) compared responding in the standard condition, described above, with three control conditions in which the square was presented at equivalent intervals but was not reliably preceded by the tone. These experiments showed that while there was an overall benefit in RT in having the tone precede the square, the linear trend in response times was determined by the recency of the square rather than by the pairing of the tone with the square. This is good evidence that the linear trend in speeded RTs is not wholly due to the strengthening and weakening of the tone-square association.

In the eyeblink variant of the Perruchet effect it is not possible to emulate the same conditions as in Mitchell et al. (2010), as the performance of the eyeblink response requires a punctate stimulus to time the response. However, another way to assess the relative contribution of response priming of eyeblink CRs, and which avoids the problems of reduced sensitivity as a result of fewer trials, is to presents the US at standard intervals signaled by a punctate stimulus, but where associative strength cannot account for the variation in responding. A differential conditioning paradigm in which one stimulus (CS+) perfectly predicts the occurrence of the US and another stimulus (CS-) predicts the absence of the US and which incorporates runs of reinforced and non-reinforced trials provides such a design. In a differential conditioning paradigm associative strength will be quickly accrued to the CS+, which is continuously reinforced, and should not be acquired by the CS-, which is never reinforced. The number of preceding CS-US trials rather than run length should be the primary influence on associative strength of the CS+ and this effect will quickly asymptote. Any effect of recent US presentations on performance can be assessed by examining responses to the CS+ and CS- as a function of the preceding trials. If recent US presentations influence CRs then responding to both the CS- and the CS+ should increase following CS-US presentations and should decrease following CS-alone presentations.

Experiment 1

This experiment used a mixed, within and between, subject design with two groups of participants receiving differential eyeblink conditioning with runs of CS-US and CS-alone trials similar to that used by Perruchet (1985). The focus of the experiment was on the factors influencing CR production. There were two groups, an "Easy" condition in which the CS+ and CS- were readily discriminable and a "Hard" condition in which they were not. If associative strength is responsible for the linear trend, then CRs should progressively increase following runs of CS-US trials and progressively decrease following runs of CS-alone trials in the Hard condition, where the CS+ and CS- are effectively perceived as a single partially reinforced stimulus. A single partially reinforced paradigm could have been used but for design reasons the comparison with the Easy condition is more straightforward when both groups nominally contain a CS+ and CS-. There should not be as strong a linear trend in the Easy condition, where associative strength should quickly accrue to the CS+ and should lanot accrue to the CS-, leading to stable differential responding to the two stimuli. If, on the other hand, recent presentations of the US prime responding and this effect declines over time, then both the Hard and Easy conditions would show greater CRs following CS-US trials than CS-alone trials, for the CS+ and CS-, as the similarity between the CSs is irrelevant because responding is not CS-driven. The predictions of a simulated associative strength model and an idealized response priming account of the Perruchet effect for the Hard and Easy conditions are illustrated in Figure 1. A basic error correcting model simulation produces the patterns shown in Panels (A) for Easy and (B) for Hard. In practice, the pattern for Easy might resemble some blend of Panels (A) and (B) because there might be some generalization between the two CSs. Nevertheless, an associative account would predict that the linear trend in the Easy condition would have a shallower gradient than the Hard condition. To try and disentangle the associative strength and response priming accounts further, predictions were also made for the effects of the variable ‘Level’ and another factor capturing whether the preceding runs contained the US or not (US absent/present). The variable Level is sensitive to whether associative strength is responsible for the increasing linear trends in each condition, because it indexes the cumulative effect of trials of a given type whilst collapsing over positive and negative trials (Destrebecqz et al., 2010; McAndrew et al., 2012). Level is constructed by averaging run lengths -3 and +1 to form level 1, runs lengths -2 and +2 to form level 2, and run lengths -1 and +3 to form level 3. As there is not a corresponding -4/+4 run length for both CS+ and CS- these run lengths are not included in the Level variable. Predictions for Level and US absent/present factors are shown on the right side of each panel. The associative account would predict an increasing linear trend over Level in the Hard condition, as well as higher responding for US present trials than US absent trials. However these effects would be expected to be weaker in the Easy condition.

(Figure 1 about here)

A response priming account would predict a different pattern, shown in Panels (C) and (D) of Figure 1 for the Easy and Hard conditions respectively. Response priming will result in an increase in CRs following the presentation of the US. That is the CR becomes easier to produce when the CS is presented following a US presentation. This may be due to the US presentation priming the US representation which in turn makes it easier for the CS to activate the US representation when the CS is presented, which results in the CR. Alternatively it may be that the emission of the UR, which is produced by the US, subsequently primes the elicitation of the CR. We would expect this priming to be fairly immediate post-US, but to require the presentation of the CS to be expressed. Furthermore, we would expect decay of this priming to be relatively rapid, and potentially precipitated by the presentation of the CS. Given these assumptions, there would be a substantial difference in CRs for US absent trials (lower) compared to US present trials (higher), with relatively little effect of Level, leading to the idealized step function shown on the left hand sides of Panels (C) and (D). This pattern is only slightly modulated by discriminability, with the Easy

CS+ showing slightly less of an increase from US absent to US present simply because of a ceiling effect in CR production. This model assumes that CS- produces a CR that can be primed. We acknowledge that priming might not be asymptotic on one trial and that the decline in response priming might be gradual, leading to an effect on the Level factor. However, only a response priming explanation can explain significant effects of US absence/presence in the absence of an effect of Level. This pattern is incompatible with an associative account.

Method

Participants

Seventy-two first year undergraduate participants (56 female) were recruited from the Western Sydney University (Sydney, Australia) to participate in this experiment. The age range of this sample was 17 to 45 years of age with a mean age of 20.7 years. All participants received research credit for their participation. There were 36 participants in both the Easy and Hard conditions. Three participants in the Hard condition were excluded from the analysis of expectancy data because they had missing data.

Apparatus and Stimuli

The CS stimuli were colored pictures, presented on a computer screen and constructed in Paint. They comprised a 5.5cm colored square presented on a black background in the center of the screen, subtending a visual angle of 5.5° at an approximate viewing distance of 57cm. In the Easy condition the CS stimuli were a blue square (51, 191, 191; Red, Green, and Blue values represent color proportions out of 255 on a standard 24bpp computer display) and a green square (51, 191, 51). For half of the participants in the Easy condition the blue square served as the CS+ and the green square served as the CS- and vice versa for the other half. In the Hard condition the CS stimuli were two subtly different blue-green squares (51, 191, 116, and 51, 191, 126). As in the Easy condition the assignment of CS stimuli to CS+ and CS- was counterbalanced across participants.

The US was a 100ms, 15psi puff of air (measured at the point of discharge) released from a pressurized tank of medical grade dry air through a modified air pressure regulator. The US was delivered to participants' left eye through a 1mm nozzle attached to 2m of plastic tubing. The nozzle was fixed to an adjustable arm which was positioned approximately 2 cm in front of the participant's left eye and was attached to the modified head mount of a welder's mask. An infrared light emitter and detector were attached above the nozzle to measure eyeblinks. The amount of infrared light detected varied according to whether the participants' eye was open or closed. A blink response was inferred from a positive deviation in the infrared light measure. The presentation of the stimuli and recording of the eyeblinks and button press responses were controlled by custom written LabView software (National Instruments) and an analogue to digital data acquisition interface card.

Participants were instructed to make an expectancy rating during the presentation of the CS on a custom made five-button device. The five levels of expectancy which participants could choose were: "Definitely no airpuff", "Might not be an airpuff", "Don't know", "Might be an airpuff" and "Definitely airpuff"; which corresponded to the five buttons on the device going from left to right. It was necessary to have participants make their expectancy ratings during the CS because the CS may influence expectancy. Participants were asked to rest their fingers over the five expectancy buttons so that they could respond quickly.

Procedure

Participants gave informed consent and were then seated in a dimly lit room in front of a 58cm ASUS HDMI LED monitor. The experimental room was separate from where the air-tank and the computer, which controlled the stimulus presentation and response recording. Participants were told that they would be shown some pictures on a computer screen and would receive some puffs of air to the eye. To allow familiarization and calibration of the recording equipment, each participant received one presentation of each visual CS and a single airpuff. The blink response to this initial airpuff presentation was recorded and was assessed to determine whether it was of sufficient magnitude to be reliably measured. If the eyeblink reflectance measure in response to the airpuff was not present or was very small, then the airpuff nozzle and the infrared sensor were adjusted to point more directly into the subject's eye, and another airpuff was presented. This process was repeated until a reliable eyeblink response was measured. Participants were then told that they would see colored squares on the computer screen and half would be followed by an airpuff. They were also asked not to promote or inhibit their blink response or close their eye for long periods of time during the experiment. The participants were asked to make an expectancy rating on every trial during the presentation of the CS by pressing one of the five buttons.

The conditioning session consisted of 157 trials, separated by an inter-trial interval that varied randomly between 10 and 15 s. Seventy-eight trials were CS+ trials where the picture was followed by the airpuff and seventy-nine were CS- trials where no airpuff was presented. The CS was presented for 1350 ms, overlapping and co-terminating with the 100-ms US in the case of the CS+. The inter-stimulus interval was therefore 1250 ms. The sequence of trials was arranged such that participants received runs of CS+ and CS- trials in the same quantity as Perruchet (1985). The number of runs of lengths 1, 2, 3, and 4 are depicted in Table 1. Four different trial orders were constructed using these runs. Two original randomized sequences were created by randomly selecting lengths of CS-US and CS-alone runs alternately. Two additional sequences were created by replacing the CS-US trials from each original sequence with CS-alone trials and vice versa.

(Table 1 about here)

After completion of the conditioning session, the participants completed a post-testing questionnaire to assess their knowledge of the stimulus contingencies. The results of this questionnaire are not reported in the interests of brevity.

<u>CR definition</u>

A CR was defined as an eyeblink made during the 500ms interval prior to US onset on CS+ trials and during an equivalent period on CS- trials (during the period 750 to 1,250ms after the CS onset). However, to be recorded as a CR the maximum amplitude of the blink had to be greater than or equal to 20% of the same participant's maximum blink amplitude during the first five US presentations of the conditioning session.

To ensure reliable measurement of CRs, trials on which the US was present but no blink could be detected during the US period, initiated either before or simultaneous with the US presentation, were removed from the analysis. Trials on which the US was not present but no blink response could be detected on the most recently presented US trial were also removed from the analysis. Approximately 2 per cent of trials were removed for this reason.

<u>Analysis</u>

The eyeblink and expectancy data were analyzed by a set of planned contrasts using a multivariate, repeated measures model (O'Brien & Kaiser, 1985). Data were first averaged by the nature of the CS (whether it was a CS+ or CS-) and also as a function of the trials immediately preceding the current trial, grouping together all trials that were preceded by a run of one, two, three or four CS-alone (designated as -1, -2, -3 and -4) or CS-US trials (designated as +1, +2, +3 and +4). The planned contrasts included a comparison of the Easy and the Hard conditions, the CS type (CS+ vs CS-), the linear trend across levels of preceding reinforcement is from -4 to +3 for the CS- and from -3 to +4 for the CS+, the Level factor and the US absent/present factor. Effect sizes were calculated for each contrast.

Bayes Factor Analysis of Linear Trends

Given our hypotheses about the linear trends observed in the Easy condition relative to the Hard, we intend to place some theoretical significance on the absence of a difference in the linear trends in the two groups, an aim that is not well-supported by classical null-hypothesis testing alone (Dienes, 2011). As such we sought to quantify the evidence in favor of the null hypothesis relative to an alternative (that the slopes in the two groups were different) using Bayes Factor tests. A Bayes Factor is the ratio of the probability of the observed data given of one hypothesis (e.g. H_0; the groups yield the same slope in CRs as a function of runs) to the probability of the data given another hypothesis (e.g. H_1; the slopes differ). It is now widely used as a means of comparing the strengths of our beliefs in the two hypotheses as it reflects the ratio of the likelihood of H_0 to H_1 given the observed data. To implement this for our hypotheses, we calculated the best-fitting affine function for the run length data points of each individual, then ran an independent samples t-test on the slopes of these functions, using the output to calculate a Bayes Factor (BF_{01}) as suggested by Rouder, Speckman, Sun, Morey, and Iverson (2009). As Rouder et al. suggest, we used the JZS prior for the alternative hypothesis, which assumes a Cauchy distribution of possible effect sizes. This technique compares the null hypothesis to an alternative hypothesis (different slopes in the two groups) using a distribution of possible group differences that assumes relatively large likelihood of small effect sizes but still assumes a somewhat larger probability of medium-to-large effect sizes than is given by a normal distribution (see Rouder et al., 2009 for further detail). Odds of 3 to 1 in favor of one hypothesis over the other are considered a lower bound for concluding moderate evidence in favor of the null ($BF_{01} = 3$) or alternative ($BF = 0.33$) hypotheses.

Results and Discussion

Eyeblink CRs

For both the Easy and Hard conditions, the percentage of CRs produced on CS+ and CS- trials is displayed as a function of preceding run in Figure 2 panels (A) and (B), respectively. That is, responding on CS+ trials is averaged across all trials that are preceded by a run of one, two or three CS+ trials (to give the points for +1, +2 and +3 shown in the plot for CS+) and for those trials preceded by a run of one, two, three or four CS- trials (to give the points for -1, -2, -3, and -4 shown in the plot for CS+). Responding on CS- trials is averaged across all trials that are preceded by a run of one, two, three or four CS+ trials (+1, +2, +3 and +4 points for CS-) and for those trials preceded by a run of one, two or three CS- trials (-1, -2 and -3 points for CS-). Visual inspection shows increasing linear trends in all conditions, though the overall difference in the number of CRs produced on CS+ and CS- trials differs substantially between conditions. Statistical analysis of the differential responding confirmed that a higher percentage of CRs were produced on CS+ trials (60.2%) than on CS- trials (44.7%), $F(1,70) = 59.66$, $p < .001$, $\eta^2_p = .460$, 95% CI [0.29, 0.58]. This effect significantly interacted with condition, $F(1,70) = 61.73$, $p < .001$, $\eta^2_p = .469$, 95% CI [0.29, 0.59]. A higher proportion of CS+ trials resulted in a CR than CS- trials in the Easy condition (64.9% and 33.7% respectively), $F(1,35) = 73.40$, $p < .001$, $\eta^2_p = .677$, 95% CI [0.47, 0.78]. However, no such effect was found in the Hard condition, $F(1,35) = 0.025$, $p = .874$, $\eta^2_p = .001$, 95% CI [0.00, 0.03] (55.5% and 55.7% on CS+ and CS- trials respectively).

(Figure 2 about here)

Statistical analysis revealed a significant increasing linear trend, $F(1,70) = 22.25$, $p < .001$, $\eta^2_p = .241$, 95% CI [0.09, 0.39]. This effect did not however interact with condition, $F(1,70) = 1.77$, $p = .187$, $\eta^2_p = .025$, 95% CI [0.00, 0.13], suggesting that the strength of the linear trends produced across run length in the Easy and Hard condition are not different.

Individually, a significant increasing linear trend across run length was found in the Easy condition, $F(1,35) = 6.31$, $p = .017$, $\eta^2_p = .153$, 95% CI [0.00, 0.36] and in the Hard condition, $F(1,35) = 16.75$, $p < .001$, $\eta^2_p = .334$, 95% CI [0.09, 0.51]. We sought to quantify the evidence in favor of the null hypothesis relative to an alternative using Bayes Factor tests. In this case, the Bayes factor comparing the null, that the mean linear slope was the same in the two groups, with the alternative hypothesis, that the slopes differed, yielded $BF_{01} = 2.48$. This indicates greater odds for the null hypothesis, however this would not conventionally be considered convincing evidence in favor of the null since the odds ratio was less than 3 to 1.

The failure to find a difference in the linear trends suggests that a mechanism which is unaffected by CS-US associations is responsible for the data patterns. However, to further examine if both CS-US associations as well as some other mechanism could be contributing to the overall result we examined the effects of Level and US-presence. Figure 2, panels (C) and (D), displays the percentage of CRs produced on CS+ and CS- trials as a function of Level and US-absent/present in the Easy and Hard conditions, respectively. Statistical analysis confirms a main effect of US-presence whereby more CRs were produced after participants experienced US-present trials (55.0%) than US-absent trials (49.8%), $F(1,70) = 15.75$, $p < .001$, $\eta^2_p = .184$, 95% CI [0.05, 0.34]. This effect did not interact with condition, $F(1,70) = 0.20$, $p = .653$, $\eta^2_p = .003$, 95% CI [0.00, 0.07], as this effect is present in both the Easy condition, $F(1,35) = 7.10$, $p = .012$, $\eta^2_p = .169$, 95% CI [0.01, 0.37], and the Hard condition, $F(1,35) = 8.65$, $p = .006$, $\eta^2_p = .198$, 95% CI [0.02, 0.40]. Additionally, a significant increasing linear trend in CRs across Level was found, $F(1,70) = 11.57$, $p = .001$, $\eta^2_p = .142$, 95% CI [0.02, 0.29]. This effect did not however interact with condition, $F(1,70) = 0.70$, $p = .406$, $\eta^2_p = .010$, 95% CI [0.00, 0.10]. Statistical analysis revealed that individually, the effect of Level approached significance in the Easy condition, $F(1,35) = 3.54$, $p = .068$, $\eta^2_p = .092$, 95% CI [0.00, 0.29], and CRs significantly increased across Level in the Hard condition, $F(1,35) = 8.39$, $p = .006$, $\eta^2_p = .193$, 95% CI [0.02, 0.40]. The failure to find a significant difference in the linear trends between the two conditions suggests that the strength of the linear trends is roughly equal in both conditions. This time, a Bayes factor analysis of the mean linear slopes for the Levels factor of the two groups yielded $BF_{01} = 4.05$, suggesting moderate evidence in favor of the null.

Expectancy

The expectancy ratings participants made as a function of run length on CS+ and CS- trials in the Easy and Hard conditions are displayed in Figure 2 panels (E) and (F), respectively. There is a clear difference in the overall ratings made on CS+ and CS- trials in the Easy and Hard conditions. Statistical analysis investigating this across the course of the experiment, confirms that across both conditions, higher ratings are made on CS+ trials (4.18) than CS- trials (2.37), $F(1,67) = 312.11$, $p < .001$, $\eta^2_p = .823$, 95% CI [0.74, 0.87]. This effect also interacts with condition, $F(1,67) = 256.41$, $p < .001$, $\eta^2_p = .793$, 95% CI [0.70, 0.84]. In the Easy condition average CS+ ratings (4.86) are drastically higher than those on CS- trials (1.41), $F(1,35) = 341.29$, $p < .001$, $\eta^2_p = .907$, 95% CI [0.84, 0.94]. In the Hard condition, although ratings on CS+ trials (3.50) are higher than those on CS- trials (3.33), the size of the difference is much smaller, $F(1,32) = 6.77$, $p = .014$, $\eta^2_p = .175$, 95% CI [0.01, 0.39].

With regards to any effects due to run length, an overall significant decreasing linear trend was found, $F(1,67) = 5.18$, $p = .026$, $\eta^2_p = .072$, 95% CI [0.00, 0.21]. However, this trend interacted with condition, $F(1,67) = 12.31$, $p = .001$, $\eta^2_p = .155$, 95% CI [0.03, 0.31]. In the Easy condition, the linear trend was not significant, $F(1,35) = 1.35$, $p = .254$, $\eta^2_p = .037$, 95% CI [0.00, 0.21], whereas in the Hard condition it was, $F(1,32) = 11.07$, $p = .002$, $\eta^2_p = .257$, 95% CI [0.04, 0.46].

The results of Experiment 1 are consistent with response priming contributing to the linear trend in CRs in the Perruchet effect. The manipulation of CS discriminability was clearly effective with significantly greater differential conditioning in the Easy than Hard condition. There was also evidence for an increasing linear trend in CRs as a function of recent reinforcement in both the Easy and Hard conditions. Critically however there was no significant interaction between the linear trend and condition. The associative hypothesis would predict an interaction between the linear trend and condition given the significant difference in the discriminability of the CS+ and CS- between conditions, however the failure to find evidence of an interaction between the linear trend and condition may simply reflect a lack of power to detect a real difference rather than the absence of any difference to detect.

The Level by US-absent/present analysis attempts to separate out associative (Level) and response priming (US absent/present) contributions. On this analysis of the CR data, we have significant effects on both US absent/present and Level factors, neither of which interact with condition. The failure to interact with condition favors the priming hypothesis, as does the strong effect of US absent/present, whereas the significant effect of Level and its similar effect size to the US absent/present factor favors the associative account. This means that both explanations can account for aspects of the results, and suggests that both may be involved. One potential weakness of Experiment 1is that the manipulation of stimulus similarity, though effective, may have nonetheless resulted in substantial stimulus generalization between the CS+ and CS- in the Easy condition. Consequently, in the next experiment we attempted to maximize the manipulation of stimulus discriminability to detect a difference on the linear trend.

Experiment 2

There are two groups in Experiment 2, a Cross-modal condition in which the CS+ and CS- are from different sensory modalities, auditory and visual, in order to maximize the discriminability between the CSs, and a Hard condition, identical to that used in Experiment 1. In the Cross-modal condition there should be little generalization between the CSs and strong differential conditioning. In this condition non-reinforced presentations of the CS- should not greatly influence the associative strength of the CS+ and likewise reinforced presentations of the CS+ should not greatly influence the associative strength of the CS-. However, in the Hard condition, where there is considerable similarity between the CS+ and CS- while still presenting two different stimuli, associative processes can strongly contribute to the run length effect. Therefore, evidence for an associative contribution on CRs in the Perruchet effect would be a stronger linear trend, particularly as a function of Level, in the Hard condition compared to the Cross-modal condition.

Method

Participants

Seventy-two first year undergraduate participants (59 female) were recruited from the University of Western Sydney (Sydney, Australia) to participate in this experiment. The age range of this sample was 17 to 50 years of age with a mean age of 20.9 years. All participants received research credit for their participation. There were 36 participants in both the Cross-modal and Hard conditions. The same trial exclusion criterion was used as in Experiment 1. This led to 3 participants in the Cross-modal and 2 in the Hard condition being excluded from the analysis of CR data because they were missing CR data. Five participants in the Cross-modal condition and 2 participants in the Hard condition were excluded from the analysis of expectancy data because they had missing expectancy data.

Apparatus and Procedure

The apparatus and procedure were the same as those used in Experiment 1 except where indicated below. The CS stimuli were an 85-dB 1000-Hz tone, and colored squares. In the Cross-modal condition the CS stimuli were a blue-green square (51, 191, 116) and a tone. In the Hard condition the CS stimuli were the same as Experiment 1. In both conditions the allocation of stimuli to role of CS+ and CS- was counterbalanced across participants.

Following conditioning participants were administered with a post-experimental questionnaire similar to that used in Experiment 1.

Results and Discussion

Eyeblink CRs

The data were treated in exactly the same way as in Experiment 1. Percentage of CRs on CS+ and CS- trials as a function of preceding run, in both the Cross-modal and Hard conditions, are displayed in Figure 3 panels (A) and (B), respectively. Increasing trends across run length can be seen in all conditions, though the percentage of CRs on CS+ and CS- trials differs between conditions. Statistical analysis of discriminative responding confirmed a larger percentage of CRs were produced on CS+ trials (57.0%) than CS- trials (45.1%) collapsed over both conditions, $F(1,65) = 34.42$, $p < .001$, $\eta^2_p = .346$, 95% CI [0.17, 0.49]. The magnitude of differential responding differed significantly between the Cross-modal and Hard conditions, $F(1,65) = 22.08$, $p < .001$, $\eta^2_p = .254$, 95% CI [0.09, 0.41]. In the Cross-modal condition, there were considerably more CRs on CS+ trials (55.1%) than CS- trials (33.7%), $F(1,32) = 31.81$, $p < .001$, $\eta^2_p = .498$, 95% CI [0.23, 0.65]. There was no evidence of differential responding in the Hard condition, $F(1,33) = 2.36$, $p = .314$, $\eta^2_p = .067$, 95% CI [0.00, 0.26].

(Figure 3 about here)

Statistical analysis on overall run length, established a significant increasing linear trend collapsed across conditions, $F(1,65) = 8.67$, $p = .004$, $\eta^2_p = .118$, 95% CI [0.01, 0.27]. This effect did not however interact with condition, $F(1,65) = 0.21$, $p = .651$, $\eta^2_p = .003$, 95% CI [0.00, 0.08]. In the Cross modal condition, a significant increasing trend in CR was identified, $F(1,32) = 5.96$, $p = .020$, $\eta^2_p = .157$, 95% CI [0.00, 0.37], though in the Hard condition this effect was only marginally significant, $F(1,33) = 3.98$, $p = .054$, $\eta^2_p = .108$, 95% CI [0.00, 0.31]. Bayes factor analysis of the mean slopes of each group yielded BF_{01}= 4.92, indicating odds in favor of the null hypothesis that the mean linear trend did not differ between groups.

The data were collapsed to form the variables Level and US-absent/present (Figure 3, panels (C) and (D)). Statistical analysis revealed a significant effect of US-absent/present, whereby a higher percentage of CRs were produced after our participants experienced US-present trials (52.2%) than US-absent trials (49.1%), $F(1,65) = 5.21$, $p = .026$, $\eta^2_p = .074$, 95% CI [0.00, 0.21]. This effect did not however interact with experimental condition, $F(1,65) = 0.36$, $p = .551$, $\eta^2_p = .005$, 95% CI [0.00, 0.09], indicating that this increasing pattern from US-absent to US-present does not differ in size between the Cross-modal and Hard conditions. But, there was no overall significant linear trend across Level, $F(1,65) = 0.98$, $p = .348$, $\eta^2_p = .014$, 95% CI [0.00, 0.12], nor any interaction between Level and condition, $F(1,65) = 0.97$, $p = .329$, $\eta^2_p = .015$, 95% CI [0.00, 0.15]. Individually neither the Cross-modal condition, $F(1,32) = 0.001$, $p = .973$, $\eta^2_p < .001$, 95% CI [0.00, 0.00] nor the Hard condition, $F(1,33) = 1.44$, $p = .238$, $\eta^2_p = .042$, 95% CI [0.00, 0.22], produced a significant trend in CRs as a function of Level. A Bayes factor test of the mean slopes of each group yielded BF_{01}= 3.47, which again indicated evidence in favor of the null hypothesis that the mean linear trend for the Levels analysis did not differ between groups. According to an associative account the US-absent/present effect would be expected to be approximately 1.5 times larger than the Level effect if we assume that the associative effect is linear across run length, as indicated by our model simulation illustrated in Figure 1. If the Level effect is adjusted on this basis (i.e. multiplied by 1.5) to be as sensitive as the US-absent/present effect overall this gives $F(1,65) = 2.21$, $p = 0.142$, , $\eta^2_p = 0.033$, 95% CI [0.00, 0.15] which is still non-significant, as are the Hard $F(1,32) = 3.24$, $p = .08$, $\eta^2_p = 0.092$, 95% CI [0.00, 0.30] and

Cross-modal conditions $F(1,32) = 0.002$, $p = .965$, $\eta^2_p = 0.0001$, 95% CI [0.00, 0.00] assessed individually.

Expectancy

The expectancy ratings participants made on CS+ and CS- trials as a function of run length can be seen in Figure 3 panels (E) and (F). As in Experiment 1 there is a clear difference in the overall expectancy ratings made on CS+ and CS- trials in both the Cross-modal and Hard conditions. Statistical analysis confirms that higher expectancy ratings are made on CS+ (4.20) than CS- trials (2.22), $F(1,63) = 1597.35$, $p < .001$, $\eta^2_p = .962$, 95% CI [0.943, 0.972] and this effect interacts with condition, $F(1,63) = 1213.27$, $p < .001$, $\eta^2_p = .951$, 95% CI [0.93, 0.96]. In the Cross-modal condition, a highly significant difference between ratings made on CS+ (4.88) and CS- (1.18) trials was found, $F(1,30) = 1800.11$, $p < .001$, $\eta^2_p = .984$, 95% CI [0.97, 0.99]. Whereas in the Hard condition, although a significant difference is still evident between ratings made on CS+ (3.51) and CS- (3.26) trials, the effect is smaller, $F(1,33) = 24.74$, $p < .001$, $\eta^2_p = .428$, 95% CI [0.17, 0.60].

With regards to whether run length modulated ratings, an overall decreasing linear trend was found, $F(1,63) = 19.38$, $p < .001$, $\eta^2_p = .235$, 95% CI [0.07, 0.39], which interacted with condition, $F(1,63) = 24.48$, $p < .001$, $\eta^2_p = .280$, 95% CI [0.11, 0.43]. This interaction reflects that in the Cross-modal condition there was not a significant linear trend across run length, $F(1,30) = 1.70$, $p = .202$, $\eta^2_p = .054$, 95% CI [0.00, 0.25], whereas in the Hard condition a significant decreasing linear trend was found, $F(1,33) = 25.00$, $p < .001$, $\eta^2_p = .431$, 95% CI [0.17, 0.60].

While the results of Experiment 2 are not conclusive, they offer some additional support for the response priming account. As in Experiment 1 there was clear evidence of differences in stimulus differentiation between the conditions, an overall significant trend in the eyeblink CRs as a function of runs, but no evidence of an interaction between the linear trend and condition. However the results of Experiment 2 differ to those of Experiment 1 in that there is an effect of the absence/presence of the US on preceding trials that is not accompanied by a significant linear trend in Level, even when the Level effect is adjusted to be as sensitive as the US absent/present effect. While the absence of the Level effect in the Cross-modal condition might be expected, the failure to replicate the Level effect in the Hard condition from Experiment 1 is somewhat surprising. The apparatus, stimuli and experimental parameters for the Hard condition in Experiment 1 and 2 were identical but the experimenters were different which may have introduced some additional variability.

A priming account would predict that whether the US has occurred recently would be the primary influence on CR probability. It might be that there is a cumulative process that grows with successive US presentations, but this does not have to be the case, and should be a minor effect compared to the difference between US absence/present. There is some evidence from studies of response curing in a spatial priming paradigm to suggest that priming is maximal after a single outcome (Jiang, Li, & Remington, 2015). If there is an effect of US-presence/absence due to associative processes, then this has to be accompanied by an effect of Level as well. Therefore the strong influence of the recent presentation of the US on eyeblink CRs in the absence of any clear influence of successive trials, provides evidence for response priming in the Perruchet effect. In our final experiment we take the logical next step of minimizing the associative contribution in both groups tested to investigate whether there is still evidence for a linear trend and a US-absent/present factor in the absence of any effect of Level.

Experiment 3

There were two groups in Experiment 3, a Cross-modal condition, similar to that in Experiment 2 where the CS+ and CS- are taken from different sensory modalities, and a Within-modal condition, where the CS+ and CS- are both from the same sensory modality but are easily distinguishable from each other (a tone and white noise). Where the CSs are easily discriminable and there is very strong differential conditioning there should be little associative contribution to any run length effect on eyeblink CRs. Evidence for a priming contribution to the run length effect on CRs in the Perruchet effect would be seen in a significant US-absent/present factor in both the Within-modal and Cross-modal conditions.

Experiment 3 differs in a number of ways from Experiments 1 and 2. Experiment 3 did not include trial-by-trial expectancy, instead participants watched a silent movie during conditioning, and the trial sequences of reinforced and non-reinforced trials were closer to that of a truly random sequence, than those used in Experiments 1 and 2. However, given that expectancy in the easy to discriminate conditions divided along stimulus lines and did not differ as a function of run length there was no reason to suspect that the presence or absence of expectancy would make any difference to CRs as a function of run length. Likewise, using a different sequence of runs of trials should be of little consequence provided the sequence contains random runs of reinforced and non-reinforced trials.

Method

Participants

One hundred and two first year undergraduate participants (80 female) were recruited from the University of New South Wales (Sydney, Australia) to participate in this experiment. The age range of this sample was 17 to 49 years of age with a mean age of 21.9 years. All participants received research credit for their participation. There were 51 participants in the Cross-modal and Within-modal conditions. Eight participants in the Cross-modal condition and 4 participants in the Within-modal condition were excluded from the analysis of CR data because they were missing CR data.

Apparatus and Procedure

The apparatus and procedure were the same as those used in Experiment 1 except where indicated below. The CS stimuli were an 85-dB 1000-Hz tone, an 80-dB white noise signal and a red square subtending a visual angle of 5.5° presented on a black background in the center of the screen. In the Cross-modal condition the CS stimuli were the tone and the picture, for half of the participants the picture was the CS+ and the tone was the CS- and for the other half of the participants this stimulus assignment was reversed. In the Within-modal condition the CS stimuli were the tone and the white noise, with the tone serving as the CS+ and the white noise the CS- for half of the participants and vice versa for the other half.

The US was a 100-ms, 15-psi puff of air (measured at the point of generation) by an eyeblink airpuff unit (San Diego Instruments, San Diego, CA). Conditioning and recording were carried out by an experimental interface (SG-500, Med Associates Inc., St. Albans, VT) connected to an Intel Pentium computer. Med-PC experimental control software was used to program the conditioning session and to record the eyeblink data.

The conditioning session consisted of 120 trials, separated by an inter-trial interval that varied randomly between 10 and 15 s. Sixty trials were CS+ trials and sixty were CS-. The sequence of trials was arranged such that participants received runs of CS+ and CS- trials in quasi-random sequence, which included at least one run of five CS+ and five CS- trials in a row and in some cases up to three such runs. Eight different trial orders were used, four original randomized sequences and four sequences created by replacing the CS-US trials with CS-alone trials and vice versa. It is possible that having participants make expectancy ratings during the CS in Experiments 1 and 2 may have interfered with CR expression and so expectancy was not recorded as part of this experiment. Instead, participants were shown a silent movie, *The Gold Rush* (Chaplin, 1925). The visual CSs were superimposed in front of the movie presentation, for the duration of the CS presentation. Following conditioning participants were asked to complete a post-experimental questionnaire assessing contingency awareness.

Results and Discussion

Eyeblink CRs

The percentage of CS+ and CS- trials on which a CR was produced as a function of run length is displayed in Figure 4, panels (A) and (B) for the Cross-modal and Within-modal conditions respectively. As in the first two experiments increasing linear trends across run length are present in each condition. However from the figure it is also clear that the overall proportion of CRs differed considerably in both conditions as a function of CS type. A standard assessment of differential responding indicated that there were more CRs produced on CS+ trials (66.3%) than CS- trials (39.6%), $F(1,88) = 135.70$, $p < .001$, $\eta^2_p = .607$, 95% CI [0.48, 0.69]. This effect interacted with condition, $F(1,88) = 9.10$, $p = .003$, $\eta^2_p = .094$, 95% CI [0.01, 0.22]. This interaction can be broken down to reveal a significantly higher percentage of CRs on CS+ trials (74.8%) than CS- trials (41.1%) in the Cross-modal condition, $F(1,42) = 76.47$, $p < .001$, $\eta^2_p = .645$, 95% CI [0.45, 0.75]. There is also evidence of discrimination in the Within-modal condition, though not to the same degree, 57.9% and 38.1% on CS+ and CS- trials respectively, $F(1,46) = 57.03$, $p < .001$, $\eta^2_p = .554$, 95% CI [0.35, 0.68].

(Figure 4 about here)

With regards to any modulation of CRs by run length, an overall significant increasing linear trend was found, $F(1,88) = 35.61$, $p < .001$, $\eta^2_p = .288$, 95% CI [0.14, 0.42]. This effect did not interact with condition, $F(1,88) = 0.09$, $p = .764$, $\eta^2_p = .001$, 95% CI [0.00, 0.04], and an increasing linear trend in CRs was found in both the Cross-modal, $F(1,42) = 18.16$, $p < .001$, $\eta^2_p = .302$, 95% CI [0.09, 0.48], and Within-modal conditions, $F(1,46) =$

17.37, $p < .001$, $\eta^2_p = .274$, 95% CI [0.08, 0.45]. A Bayes factor analysis of the mean slopes of each group yielded $BF_{01} = 5.93$, which, suggests odds in favor of the null hypothesis. The data was subsequently collapsed to form the variables Level and US-presence/absence, though note that for consistency with Experiments 1 and 2 the variable Level did not include data for run lengths over 3 (Figure 6 panels (C) and (D)). Statistical analysis revealed a main effect of US-presence, $F(1,88) = 26.51$, $p < .001$, $\eta^2_p = .232$, 95% CI [0.09, 0.37], whereby a larger percentage of CRs was produced after runs of US-present trials (56.2%) than US-absent trials (50.3%). This effect did not however interact with condition, $F(1,88) = 0.58$, $p = .448$, $\eta^2_p = .007$, 95% CI [0.00, 0.08], as this effect is present in both the Cross-modal, $F(1,42) = 12.16$, $p = .001$, $\eta^2_p = .224$, 95% CI [0.04, 0.41], and Within-modal data, $F(1,46) = 14.98$, $p < .001$, $\eta^2_p = .246$, 95% CI [0.06, 0.43]. Our analyses did not reveal any significant effects of Level in this experiment, $F(1,88) = 0.14$, $p = .712$, $\eta^2_p = .002$, 95% CI [0.00, 0.05], in either of the Cross- or Within-modal conditions, $F(1,42) = 0.48$, $p = .494$, $\eta^2_p = .011$, 95% CI [0.00, 0.14], and $F(1,46) = 0.91$, $p = .346$, $\eta^2_p = .019$, 95% CI [0.00, 0.15], respectively. Once again, the Bayes factor test revealed odds in favor of the null hypothesis that the slopes did not differ between groups ($BF_{01} = 3.32$). When the overall Level effect is adjusted to be as sensitive as the US-presence/absence effect $F(1,88) = 0.32$, $p = .576$, $\eta^2_p = 0.004$, 95% CI [0.00, 0.07], it is still non-significant, which is also the case for the Cross-modal, $F(1,42) = 1.08$, $p = .305$, $\eta^2_p = 0.025$, 95% CI [0.00, 0.17], and Within-modal conditions, $F(1,46) = 2.05$, $p = .159$, $\eta^2_p = 0.043$, 95% CI [0.00, 0.19], assessed separately.

The results of Experiment 3, like those of Experiment 1 and 2, show evidence for a linear trend in eyeblink CRs as a function of recent reinforcement history. However, both the Cross-modal and Within-modal discrimination conditions in Experiment 3 employ a CS+ and a CS- that are easily discriminable from each other which should reduce the contribution of associative learning processes to the linear trend compared to the standard Perruchet effect, in which a single CS is partially reinforced. The results of Experiment 3 show evidence for an effect of the absence/presence of the US on preceding trials that is not accompanied by a significant linear trend in Level, even when the Level effect is adjusted to be as sensitive as the US-absent/present effect. This result suggests that response priming may be contributing to the linear trend as a function of recent reinforcement history, as the likelihood of CR should be particularly influenced by whether the US has occurred recently or not according to this theory.

General Discussion

Across three experiments, when responding to CSs in a differential conditioning paradigm is assessed as a function of the preceding run of either reinforced or non-reinforced trials, we see evidence for a linear trend in eyeblink CRs, with trials following reinforced runs showing a higher probability of CRs than trials following non-reinforced runs. The strength of the linear trend did not differ significantly as a function of the discriminability of the CS+ and the CS- in any of the three experiments. There was however good evidence that the discriminability of the CS+ and CS- significantly affected the extent of differential conditioning in each of the three experiments. When the slope of the linear trend in each of the experiments is separated into the effects of recent reinforcement or non-reinforcement (US-absent/present) and successive trial order effects (Level), then there appears to be a somewhat different pattern of responding across the three experiments. In Experiment 1 there was evidence for both the Level and the US-absent/present factor contributing to the linear trend in CRs and this did not differ significantly between groups. However, in Experiments 2 and 3, where the average degree of discriminability between the CS+ and the CS- was greater than that in Experiment 1, there was clear evidence for a significant effect of the US-absent/present factor but no evidence for an effect of the Level factor.

In order to further assess the pattern of results across experiments we conducted a combined analysis of the results in which Experiment was included as a between subjects factor and Level and US-absent/present were included as within subject factors. This analysis revealed a main effect of Level across the three experiments $F(1,223) = 4.51$, $p = .035$, $\eta^2_p = .020$, 95% CI [0.00, 0.07]. Furthermore there was an interaction between Level and Experiment $F(2,223) = 3.26$, $p = .040$, $\eta^2_p = .028$, 95% CI [0.00, 0.08], indicating that the Level effect was significantly greater in Experiment 1 than Experiment 3. We hypothesize that this is due to the similarity between the CS+ and the CS- being much higher in both groups tested as part of Experiment 1 than the groups tested in Experiment 3. There was also a main effect for the US-absent/present effect $F(1,223) = 41.44$, $p < .001$, $\eta^2_p = .157$, 95% CI [0.08, 0.24]. However, there was no interaction between the US-absent/present effect and Experiment $F(2,223) = 1.21$, $p = .299$, $\eta^2_p = .011$, 95% CI [0.00, 0.05].

What does this pattern of results suggest about the processes underlying the pattern of CRs in the three experiments? An associative account based on CS-US associations would predict that both the immediately preceding type of reinforcement as well as the number of successive trials of a particular reinforcement type would influence the probability of CRs. Thus, it would predict that both the recency of presentation of the US (US-absence/presence) and the number of preceding reinforced or non-reinforced trials (Level) should influence the probability of CRs. Importantly, according to an associative account if there is an effect of US-presence/absence effect, then this *has to be accompanied* by an effect of Level as well. However, a priming hypothesis would predict that the recency of the US would be the primary influence on CR probability. In Experiments 2 and 3 the significant influence of the recent presentation of the US on CRs in the absence of any effect of successive trial presentations (as indexed by the Level factor) suggests that response priming rather than changes in the strength of the CS-US association is contributing to the linear trend in CRs as a function of the preceding run in these experiments.

Furthermore, an associative account would predict that there would be differences in the strength of the linear trend as a function of the degree of discriminability between the CS+ and the CS-. This is because the extent to which there is generalization between the CS+ and the CS- will influence the extent to which CS-US and CS-alone presentations will produce increments and decrements in associative strength. When generalization is high then responding to both the CS+ and CS- will be moderate and runs of CS-US trials will continue to produce increments and runs of CS-alone trial will continue to produce decrements throughout conditioning. When generalization is low then responding to the CS+ will be high and responding to the CS- will be low and this will limit the increments and decrements in associative strength as a result of runs of the CS-US and CS-alone trials. In the Hard conditions in Experiments 1 and 2 there was almost complete generalization between the CS+ and CS-. In the Easy condition of Experiment1, and the Cross- and Within-modal conditions of Experiments 2 and 3 there is less generalization than in the Hard condition, although the extent of the generalization in each of these conditions does appear to be non-negligible. Previous evidence from studies of human eyeblink conditioning indicate that while there is considerable generalization between stimuli within the same modality, physical similarity is the most important variable controlling differential conditioning and by implication stimulus generalization (Gynther, 1957). The results from our experiments are consistent with this in that there are significant differences in the degree of discriminative responding between the Easy and Hard conditions in Experiment 1, between the Cross-modal and Hard conditions in Experiment 2 and between the Within- and Cross-modal conditions in Experiment 3. Despite there being clear evidence of differences in discriminability of the CS+ and CS- between conditions in all three experiments there was no evidence for a significant difference in the gradient of the slope between conditions.

However, a response priming account would predict that stimulus similarity would not affect the slope of the linear trend of CRs as a function of preceding runs of reinforced and non-reinforced trials, because in a response priming account responding is hypothesized to be driven by the presence or absence of the US and unaffected by stimulus similarity. In Experiments 2 and 3 there is little effect of stimulus similarity on the gradient of the slope between conditions in these experiments. Furthermore, in Experiments 2 and 3 there is clear evidence of a strong effect of the US-absence/presence factor in the absence of any effect of successive trial presentations (as indexed by the Level factor), this suggests a response priming mechanism is largely responsible for the pattern of CRs and is largely incompatible with an associative process. Additionally, the across experiment comparison reveals that there is a strong effect of the US-absence/presence factor across all three experiments and this does not interact with Experiment as a factor, but the effect of Level is weaker and does interact with Experiment. Given that average similarity of the stimuli decreases across the three experiments it suggests that stimulus similarity is affecting the Level effect but is not influencing the US-absence/presence factor. This result suggests that associative processes are influencing the Level effect and that response priming is primarily affecting the US-absence/presence factor, because the Level effect is influenced by stimulus similarity and the US-absence/presence factor is not. This suggests that the linear trend in CRs seen in the eyeblink variant of the Perruchet effect is determined by multiple processes and has contributions from response priming *and* from changes to CS-US associations. While the associative contribution seen in Experiments 2 and 3 appears to be quite weak, the pooled data from ten independent groups trained on standard single cue Perruchet effect sequence reported in Perruchet's (2015) review show that the Level effect is generally present in the standard single cue Perruchet effect in eyeblink conditioning. The presence of a robust Level effect in the pooled data in conjunction with the Level effect in Experiment 1 and a decrease in the Level effect across experiments as stimulus similarity decreases makes a case for there being an associative contribution to the Perruchet effect in this paradigm.

In the present experiments there is good evidence for response priming, which may also contribute to demonstrations of the Perruchet effect in other paradigms, such as the dissociation of reaction times (RT) and expectancy seen in binary choice and go/nogo tasks. The results of the study by Mitchell et al. (2010) showing that the Perruchet effect could be obtained in an RT version of the paradigm even when no CS was presented can be readily explained if response priming is driving the changes in reaction time. A traditional sensitization hypothesis makes little sense in this case because the outcome (whether a square was presented on screen or not) hardly qualifies as a US that might produce a stronger CR as a consequence of exposure to it. An account that simply postulates that having emitted a response (pressing a key in this case) facilitates making that response on the next trial is a much better fit to the data and to the experimental paradigm. There is evidence to suggest that this facilitation decays over time, so that runs of -ve trials progressively reduce the effect, but that a single +ve trial is enough to give the full or near to full effect (Verbruggen, McAndrew, Weidemann, Stevens, & McLaren, 2016).

According to a response priming process the recent occurrence of an eyeblink response increases the likelihood of a subsequent punctate stimulus eliciting a CR. That is, the threshold for the CR to occur may in some sense be lowered by the recent occurrence of an eyeblink response and so make it more likely for the CR to subsequently occur. In the present differential conditioning design, where the occurrence of the response is likely to coincide with the presentation of the US, particularly under conditions with good discriminative responding, then stimulus priming and response priming are difficult to distinguish. Both accounts, however, have difficulty in explaining the failure of previous attempts to find evidence of a non-associative contribution to the Perruchet effect. In particular, the failure of Perruchet's (1985) control condition to find evidence that recent US presentations had any effect on CRs is problematic for stimulus priming and response priming hypotheses. As mentioned previously, we can speculate that this may be because the explicit unpairing of the CS and the US led to the acquisition of conditioned inhibition which masked any potential effects of US sensitization or response priming. The failure of Weidemann et al. (2009) to find any evidence of recent presentation of US-alone and blank trials on responding to a partially reinforced CS would not be predicted by stimulus priming or response priming. There is, however, some evidence in the literature to suggest that the US can have a performance effect on CRs. For example, Kimble, Mann and Dufort (1955), Dufort and Kimble (1958) and Loess (1964) all found that unpaired presentations of the US could increase responding to a CS that had previously been paired with the same US.

Across the three experiments there is a striking and complex relationship between expectancy and CRs. In the Hard conditions in Experiments 1 and 2, where the vast majority of participants could not reliably distinguish between the CS+ and the CS-, participants' expectancy was largely influenced by the preceding sequence of CS-US and CS-alone trials, as was CR production, but CRs show the exact opposite pattern to that of expectancy. In the Easy condition in Experiment 1 and Cross-modal condition in Experiment 2 the expectancies reflect the contingencies in play with expectancy near ceiling on CS+ trials irrespective of the preceding run length, and the expectancy near floor on CS- trials, also not appreciably affected by run length. This sensitivity to the contingency in the expectancy data is reflected in the CR data with significantly greater CRs to the CS+ than the CS- in both of these groups. Previous findings in differential human eyeblink paradigms have indicated a causal role for cognitively mediated expectancy in producing differential responding (Weidemann & Antees, 2012; Weidemann, Best, Lee, & Lovibond, 2013). If expectancy is influencing CR production, rather than just correlated with it, then it can account for the differential conditioning without any difficulty. However, while expectancy for the CS+ is close to ceiling and expectancy for the CS- is close to floor, this is not the case for the CRs. Responding to the CS- is elevated above floor, but not appreciably above a baseline level of blinking commonly seen in a context where unsignalled USs are being presented (e.g. Perruchet, 1985, Experiment 2; Weidemann, et al., 2013), while responding to the CS+ is well below ceiling but similar to other published studies of human eyeblink conditioning (Weidemann & Antees, 2012). Furthermore, CRs in the Easy, Within-modal and Cross-modal conditions are appreciably affected by the preceding run type while expectancy is not. From this pattern of results we conclude that while expectancy may play a causal role in differential responding, it clearly does not play a causal role in the effect of preceding runs on CRs.

Conclusion

In conclusion, across three experiments we have shown that the linear trend in eyeblink CRs as a function of preceding runs, which is seen in the Perruchet effect, can be obtained in a differential conditioning paradigm, both when the CS+ and CS- are difficult to discriminate and also when they are easy to discriminate. These results provide the first evidence that there is a contribution to the behavioral response in the eyeblink variant of the Perruchet effect that is not driven by fluctuations in the strength of CS-US associations. This non-associative contribution is most probably due to priming of the eyeblink response, and is most clearly indexed by an analysis in terms of the US-Presence/Absence factor. However, our results are compatible with the possibility that associative learning also contributes to the pattern of behavioral responses as a function of run length.

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Table 1. Organization of trials in Experiment 1 and 2.

Variable	CS alone (CS-)				CS – US paired (CS+)			
Run length	4	3	2	1	1	2	3	4
Number of runs	3	6	12	24	24	12	6	3
Number of trials	12	18	24	24	24	24	18	12

Note. The run length refers to the number of trials CS- or CS+ presented consecutively.

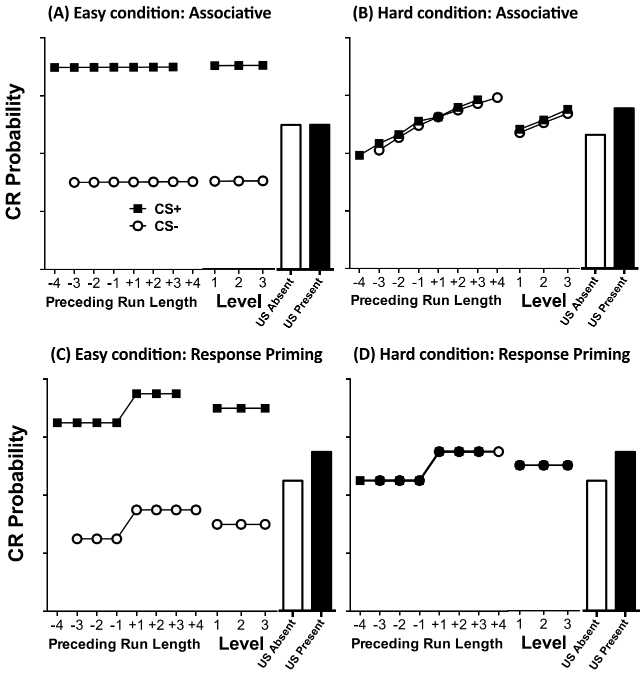


Figure 1. Hypothesized probability of a CR to the CS+ and CS- as a function of the nature and length of the preceding run in the Easy and Hard conditions, as a function of Level and as a function of the US being absent or present on the preceding trial according to an associative and response priming account of the Perruchet effect. (A) Shows the predictions of an error correction model simulation of the associative account of the Perruchet effect for the Easy condition. (B) Shows the predictions of an error correction model simulation of the associative account for the Hard condition. (C) Shows the predictions of a response priming account of the Perruchet effect for the Easy condition. (D) Shows the predictions of a response priming for the Hard condition. The simulations of the associative account were generated using a basic error correction model that used the logistic activation function to feed activation forwards from the input to output layer. Learning occurred through back propagation of error correction (Rumelhart, Hinton, & Williams, 1985). The model consisted of 21 input units, 10 hidden units and 1 output unit representing activation of the US. Each CS was represented across all input units using a Gaussian distributed pattern of activation (McLaren & Mackintosh, 2002), in order to manipulate stimulus similarity along a dimension. In the 'Easy' simulation the peak of the distribution fell at unit 5 to represent the CS+ and unit 15 for the CS-. In contrast, in the 'Hard' simulation the distributions peaked at similar points, 10 and 10.1 respectively for the CS+ and CS-. The model was run 36 times using the four sequences presented to participants in this experiment. Input activation varied on each trial consistent with the presentation of the CS+ or CS-. The inner mechanics of the model i.e. feed forward activation and back propagation, were looped in order to provide the opportunity for learning as only one iteration of the model provides minimal learning to develop. The loop lasted for 50 iterations in an attempt to capture the presentation of the CS in these experiments.

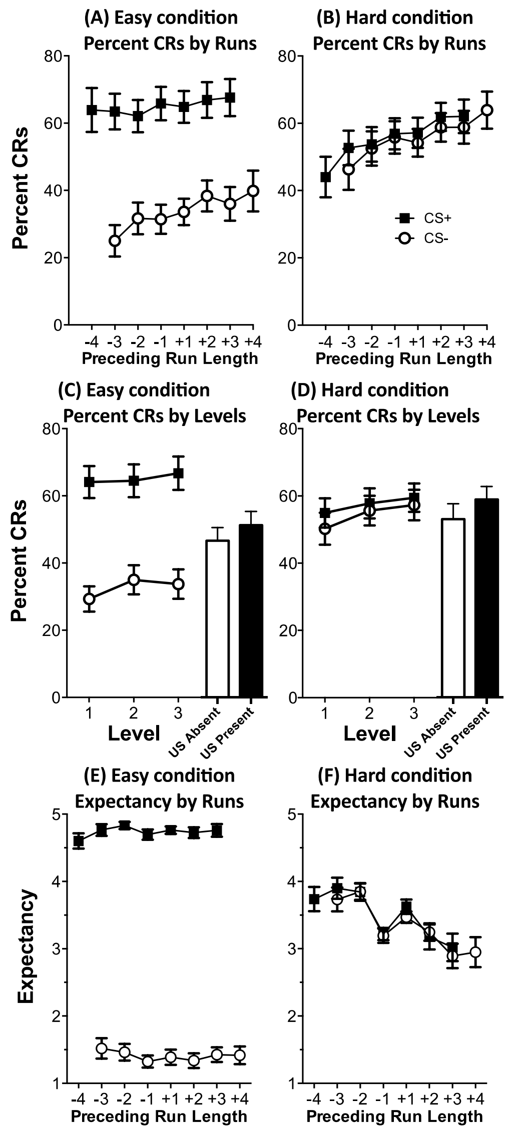


Figure 2. Mean percentage of CRs (+/- SEM) and average expectancy ratings (+/- SEM) for Experiment 1. (A) Mean percentage CRs for the CS+ and CS- as a function of the preceding run of trials in the Easy condition and (B) in the Hard condition. The number of the preceding run represents the quantity of the trials of the same type, which have been presented consecutively, where the non-reinforced runs are indicated by a minus sign (-) and the reinforced trials are indicated by a plus sign (+). (C) Mean percentage CRs for the CS+ and CS- as a function of Level in the line graph and as a function of US Absent and US present in the bar graph in the Easy condition and (D) in the Hard condition. (E) Average expectancy ratings for the CS+ and CS- as a function of the preceding run of trials in the Easy condition and (F) in the Hard condition.

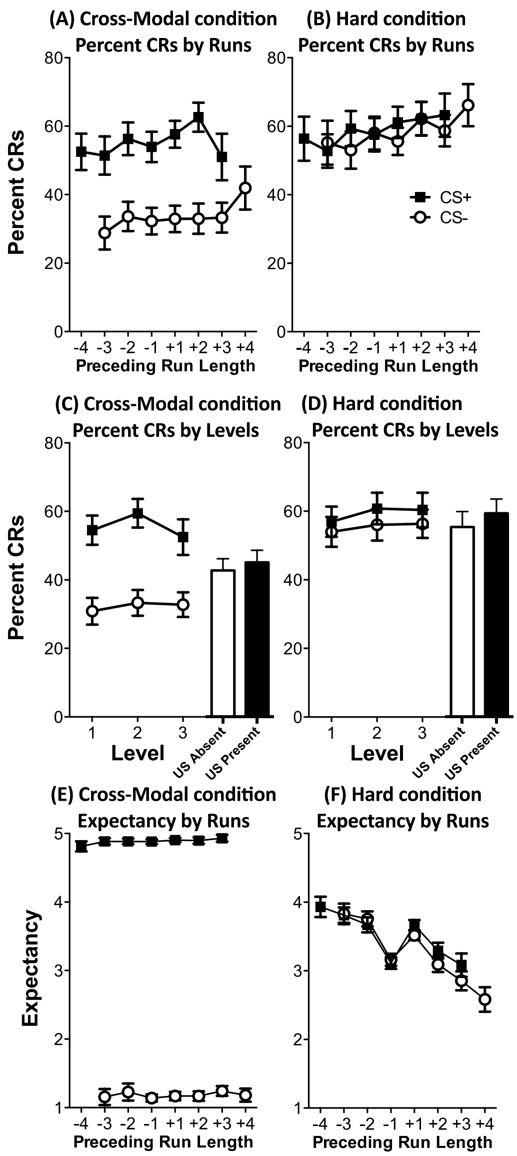


Figure 3. Mean percentage of CRs (+/- SEM) and average expectancy ratings (+/- SEM) for Experiment 2. (A) Mean percentage CRs for the CS+ and CS- as a function of the preceding run of trials in the Cross-modal condition and (B) in the Hard condition. (C) Mean percentage CRs for the CS+ and CS- as a function of Level in the line graph and as a function of US Absent and US present in the bar graph in the Cross-modal condition and (D) in the Hard condition. (E) Average expectancy ratings for the CS+ and CS- as a function of the preceding run of trials in the Cross-modal condition and (F) in the Hard condition.

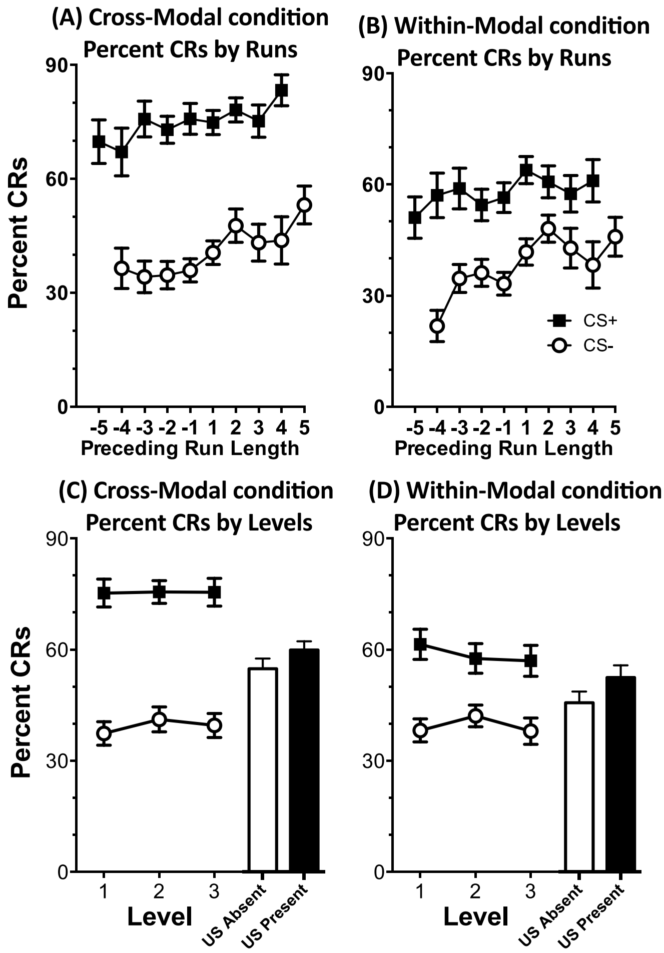
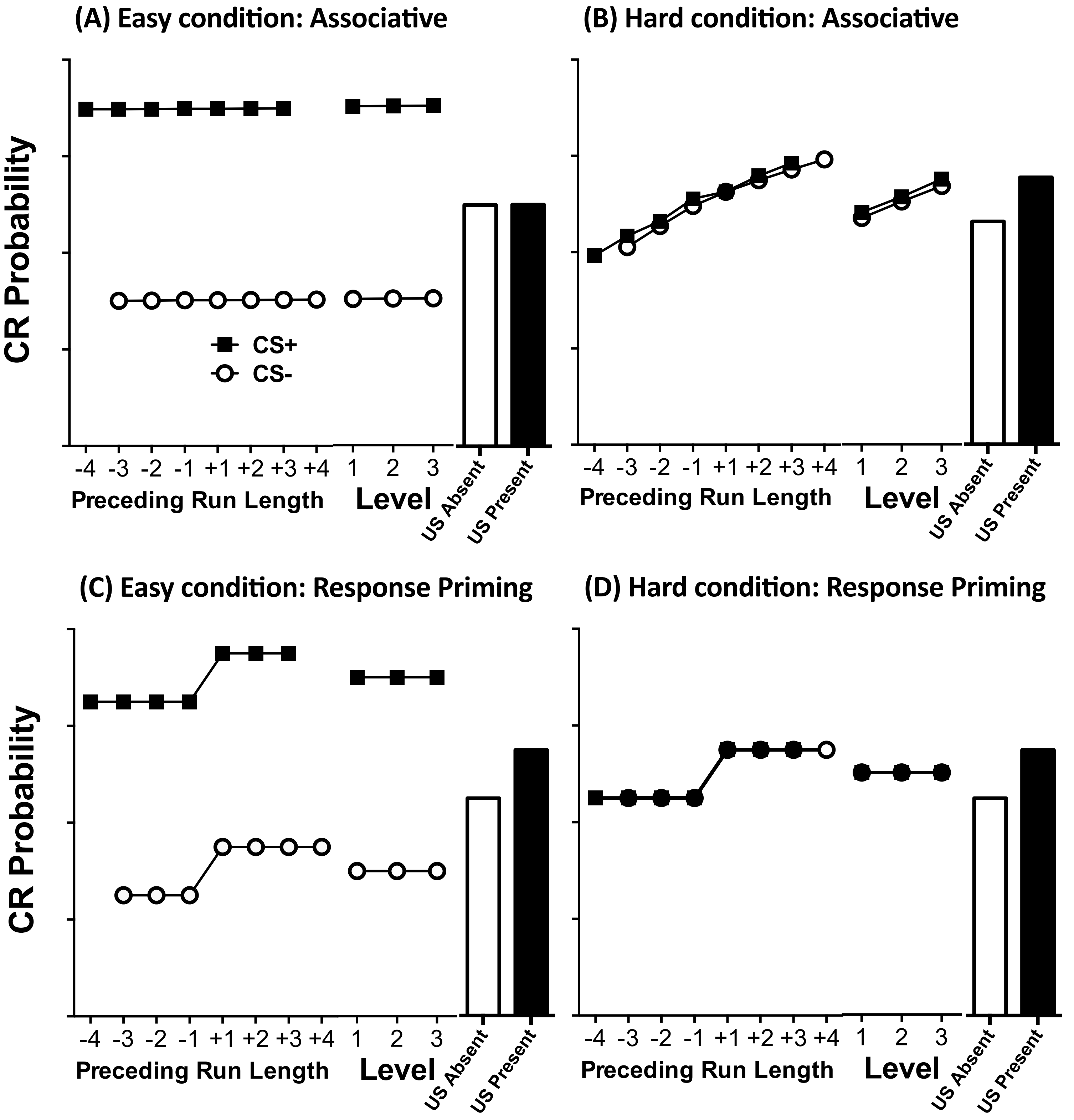


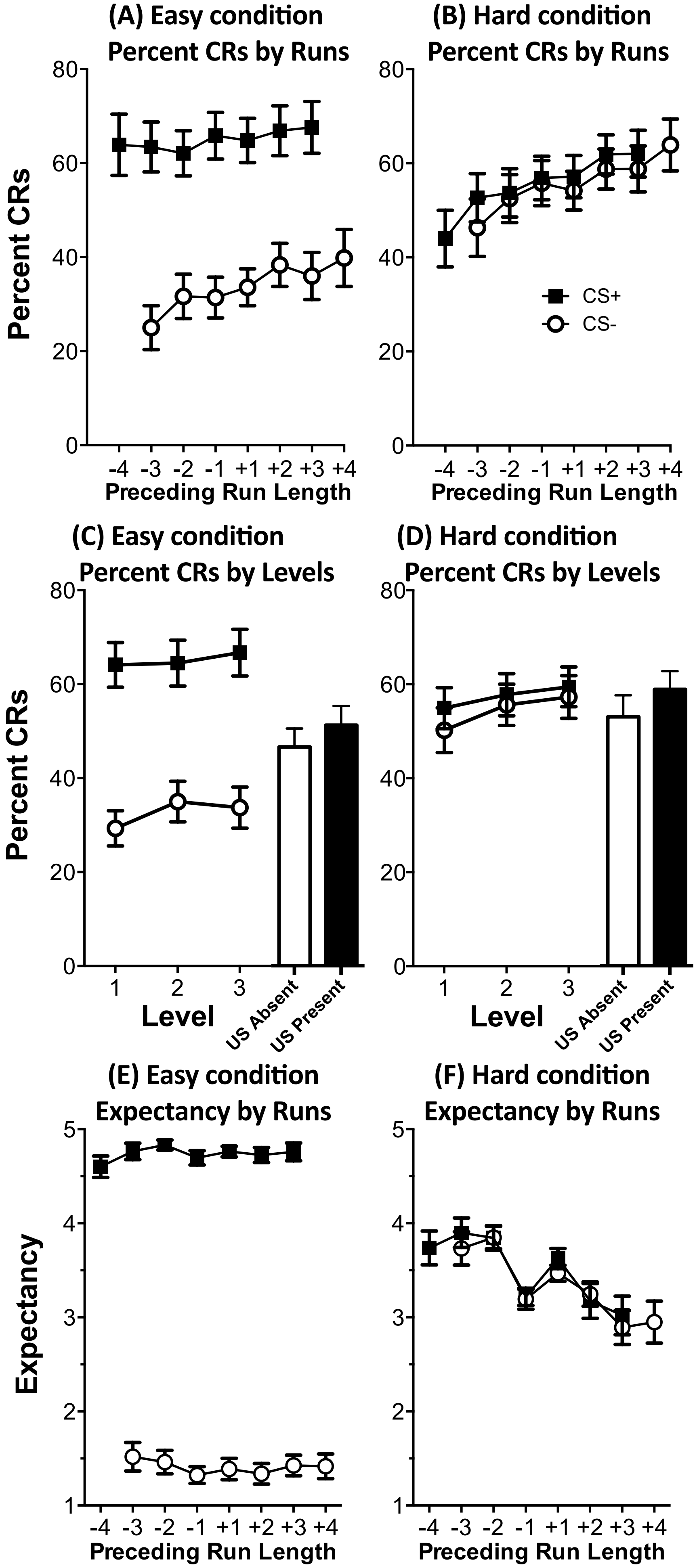
Figure 4. Mean percentage of CRs (+/- SEM) for Experiment 3. (A) Mean percentage CRs for the CS+ and CS- as a function of the preceding run of trials in the Cross-modal condition and (B) in the Within-modal condition. (C) Mean percentage CRs for the CS+ and CS- as a function of Level in the line graph and as a function of US Absent and US present in the bar graph in the Cross-modal condition and (D) in the Within-modal condition.

Figure

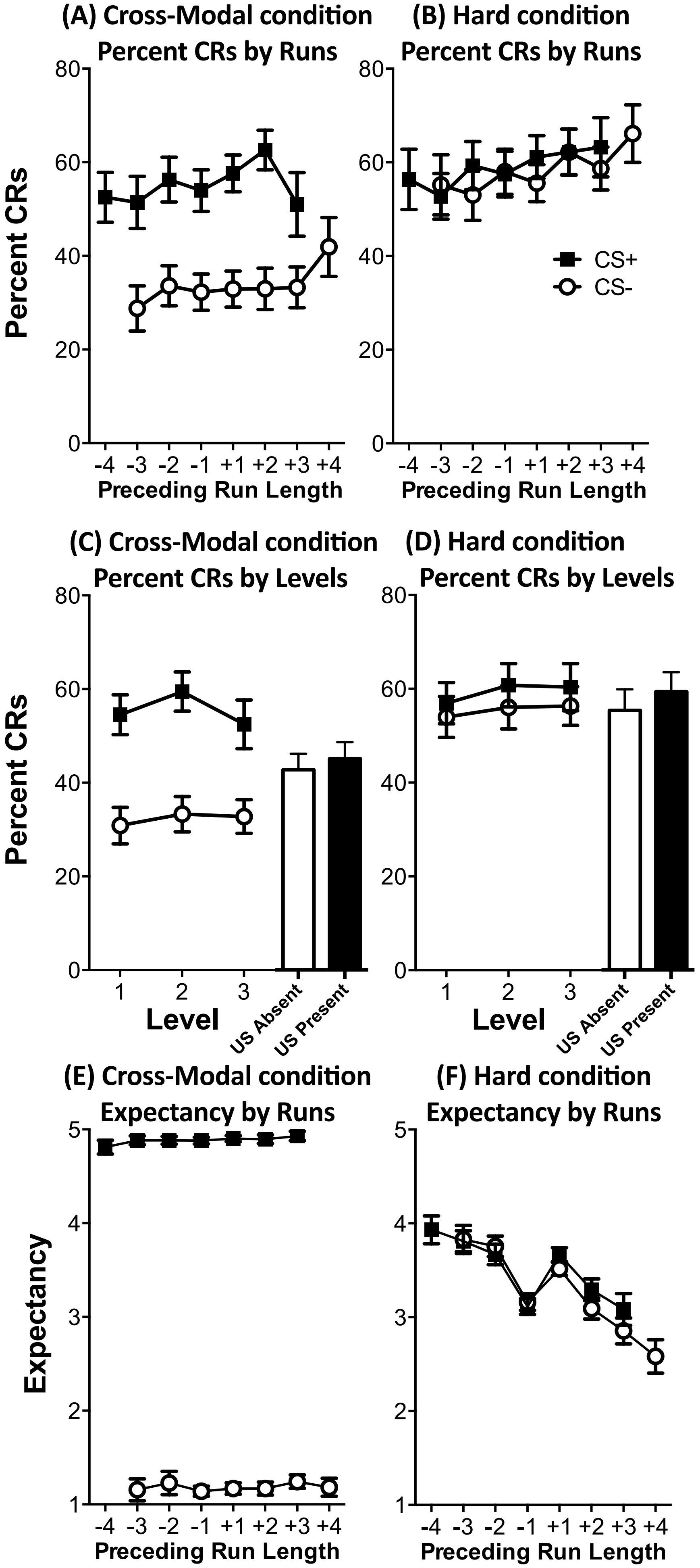


(A) Easy condition: Associative
(B) Hard condition: Associative
(C) Easy condition: Response Priming
(D) Hard condition: Response Priming
CR Probability
CS+
CS-
-4 -3 -2 -1 +1 +2 +3 +4
Preceding Run Length
1 2 3
Level
US Absent
US Present

Figure

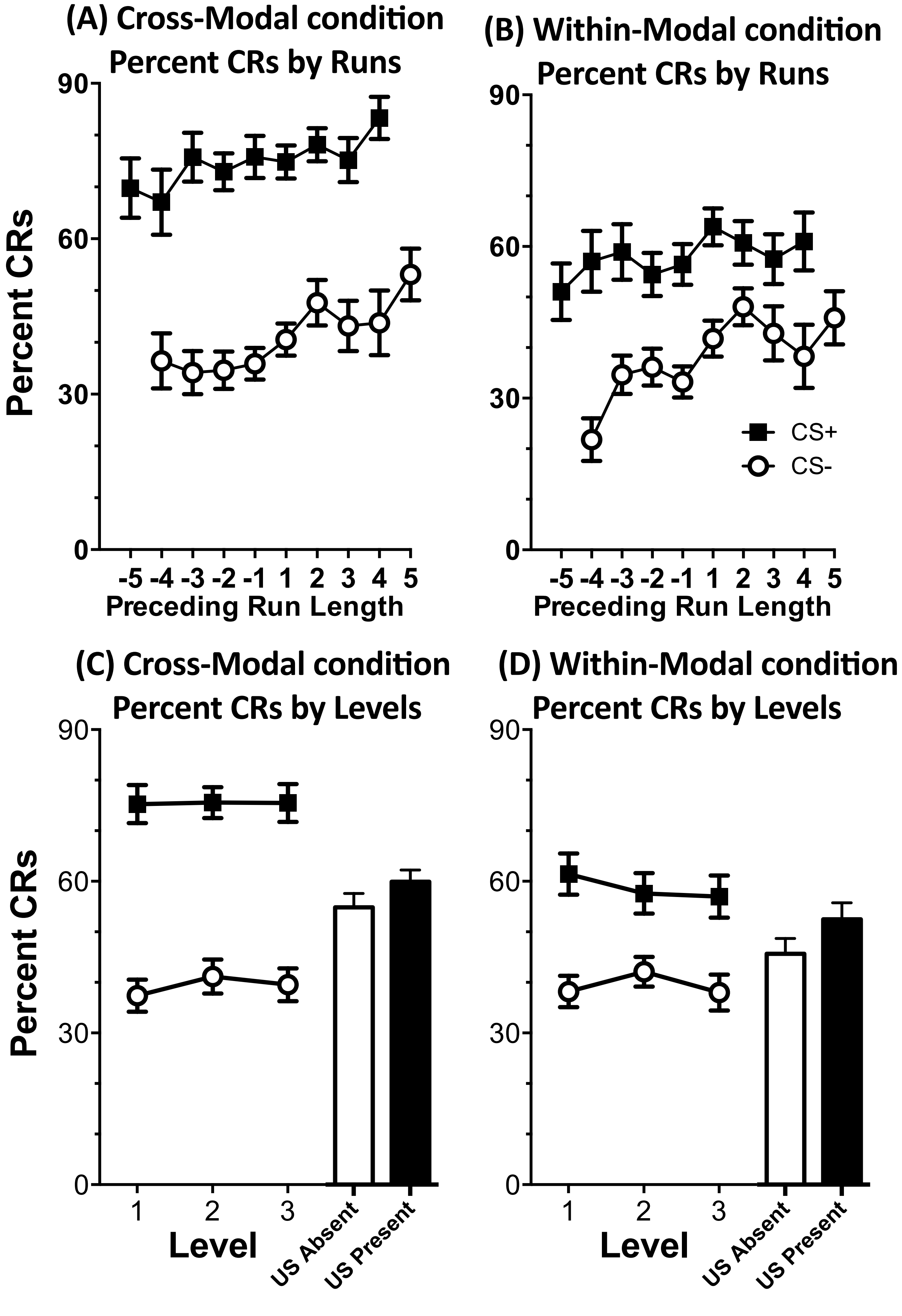

(A) Easy condition
Percent CRs by Runs
(B) Hard condition
Percent CRs by Runs
Percent CRs
0
20
40
60
80
-4 -3 -2 -1 +1 +2 +3 +4
Preceding Run Length
CS+
CS-
(C) Easy condition
Percent CRs by Levels
(D) Hard condition
Percent CRs by Levels
1
2
3
Level
US Absent
US Present
(E) Easy condition
Expectancy by Runs
(F) Hard condition
Expectancy by Runs
Expectancy
1
2
3
4
5

Figure



(A) Cross-Modal condition
Percent CRs by Runs
(B) Hard condition
Percent CRs by Runs
Percent CRs
80
60
40
20
0
-4 -3 -2 -1 +1 +2 +3 +4
Preceding Run Length
CS+
CS-
(C) Cross-Modal condition
Percent CRs by Levels
(D) Hard condition
Percent CRs by Levels
1
2
3
US Absent
US Present
Level
(E) Cross-Modal condition
Expectancy by Runs
(F) Hard condition
Expectancy by Runs
Expectancy
5
4
3
2
1

Figure


(A) Cross-Modal condition
Percent CRs by Runs
Percent CRs
Preceding Run Length
(B) Within-Modal condition
Percent CRs by Runs
CS+
CS-
Preceding Run Length
(C) Cross-Modal condition
Percent CRs by Levels
Percent CRs
Level
US Absent
US Present
(D) Within-Modal condition
Percent CRs by Levels
Level
US Absent
US Present