



The role of US recency in the Perruchet effect in eyeblink conditioning



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ABSTRACT

In the Perruchet effect, there is a concurrent dissociation between participants' conditioned responses (CRs) and their expectancy of the unconditioned stimulus (US) across runs of repeated trials. The effect has been taken as evidence for multiple learning processes, but this conclusion follows only if the CR trend is the result of learning. Two experiments examined the role of US recency in generating the observed CR trend. A standard Perruchet condition was compared with a control condition in which US recency was controlled by presenting the US on every trial. The associative contribution was maintained by varying the temporal relationship between the CS and the US. In both experiments the pattern of CRs seen in the Perruchet condition was absent in the control condition, suggesting that the eyeblink trend in the Perruchet effect may be due to a non-associative performance factor such as priming or sensitization arising from recent US presentations.

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1. Introduction

In human Pavlovian conditioning, a neutral stimulus (conditioned stimulus, CS; e.g., a tone) is paired together with a biologically significant stimulus (unconditioned stimulus, US; e.g., a puff of air to the eye), which results in the acquisition of a reflexive response (conditioned response, CR; e.g., a blink to the tone). At the same time participants also develop an expectancy for when they think the US is going to occur. Whether these two learned responses are the result of two separate learning processes or a single integrated process is a topic of much debate (Mitchell, De Houwer, & Lovibond, 2009). Some suggest there are two separate learning systems operating during Pavlovian conditioning (see McLaren et al., 2014, for a recent review). One system resulting in conscious declarative knowledge about the contingency between stimulus events and conscious expectancy for the occurrence of the US. The other system involves the automatic formation of excitatory connections between the CS and US nodes as a result of their co-activation. Evidence for two separate learning systems would be provided by the acquisition of CRs in the absence of conscious contingency knowledge or CR production that diverges from conscious US expectancy.

Claims of such dissociations between contingency knowledge and conditioned responding are common in the human Pavlo-

vian conditioning literature. For example, Schultz and Helmstetter (2010) reported evidence of unaware electrodermal CRs, and Clark and Squire (1998) reported evidence of eyeblink CRs independent of contingency awareness, to name just two. However, a systematic review of this literature found that the majority of research is consistent with the view that awareness is necessary but not sufficient for conditioned performance (Lovibond & Shanks, 2002). When reports of conditioning in the absence of contingency awareness have been investigated, they have on occasion been found to be difficult to reliably reproduce (e.g. Lovibond, Liu, Weidemann, & Mitchell, 2011). Other instances of conditioning in the absence of awareness have been shown to arise from some other predictable feature of US occurrence, such as restrictions in the trial sequence (e.g. Singh, Dawson, Schell, Courtney, & Payne, 2013). Whether conditioning in the absence of awareness can be reliably demonstrated under conditions of adequate power and with valid and sensitive measures of awareness remains to be seen. The majority of the current evidence is consistent with the view that conditioned responding aligns with explicit beliefs, supporting a single learning system.

An important exception to this conclusion is the reliable double dissociation of CRs and US expectancy that was originally demonstrated by Perruchet (1985) in human eyeblink conditioning. Perruchet (1985) found that in a partial reinforcement paradigm, when participants' responses were assessed as a function of the preceding sequence of trials, expectancy for the US was at its highest following a series of CS-alone trials and at its lowest following a series of CS-US trials. By contrast, CRs were at their

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highest following a series of CS-US trials and at their lowest following a series of CS-alone trials. That is, that CR probability was greatest when US expectancy was lowest and CR probability was lowest when US expectancy was highest. This dissociation has been reliably reproduced in the eyeblink conditioning procedure in other labs (Weidemann, Broderick, Lovibond, & Mitchell, 2012; Weidemann, Tangen, Lovibond, & Mitchell, 2009) and has also been demonstrated in electrodermal conditioning (McAndrew, Jones, McLaren, & McLaren, 2012; McAndrew, Weidemann, & McLaren, 2013) and associative priming (Destrebecqz et al., 2010; Perruchet, Cleeremans, & Destrebecqz, 2006). The so-called Perruchet effect is consistent with dual-system theories of human conditioning but represents a challenge to single system theories which predict that CRs and US expectancy should be correlated.

However, the Perruchet effect only represents evidence for multiple learning systems if the changes in CRs and expectancy across runs of trials are the result of *learning* – that is, changes in associative strength. An alternative explanation is that the pattern of CRs reflect a non-associative or *performance* effect such as sensitization or priming arising from recent presentations of the US or recent elicitation of the unconditioned response (UR). In the Perruchet design there is a perfect confound between recency of the US and recency of CS-US pairings. For example, a run of four CS-alone trials entails both low recency of CS-US pairings and low recency of the US. Consequently, it is possible that the linear trend in eyeblink CRs as a function of recent reinforcement history could be due to the recency of US presentations and not to changes in associative strength.

Perruchet (1985) recognized that the pattern of CRs may result from a performance factor. He examined this possibility by testing a control group in which the CS and the US were never paired and instead the US was presented alone in the place of the CS-US pairings. There was evidence of a significant linear trend in the experimental group but not in the control group, leading Perruchet (1985) to conclude that the linear trend in CRs in the standard Perruchet design is due to changes in associative strength. However he did not directly compare the linear trend between groups through an interaction test. Additionally, the ability to detect changes in CRs in the control group may have been impaired due to a floor effect. Since the CS and the US were explicitly unpaired in the control group the CS could have become a conditioned inhibitor. Thus the CS may have suppressed any responding that the US-alone presentations would otherwise have caused, masking the possibility of seeing changes in eyeblink responding.

To further test the possibility that the linear trend in the Perruchet effect is the result of a non-associative performance effect, Weidemann, Tangen, Lovibond, and Mitchell (2009) examined the effect of runs of US-alone and blank trials, during which no stimuli were presented, interspersed amongst runs of CS-US and CS-alone trials. In two experiments the standard positive linear trend in eyeblink CRs was observed following runs of CS-US and CS-alone trials but this linear trend was not present following runs of US-alone and blank trials. This outcome failed to support the idea that the pattern of eyeblink responding in the Perruchet design arises from a performance factor. However, in both these experiments there were relatively few runs of US-alone and blank trials compared to the predominant runs of CS-US and CS-alone trials. Additionally, responding following runs of US-alone and blank trials could only be assessed at the end of the run when a CS-alone or CS-US trial was presented, thus further reducing the opportunity to assess the effects of these run sequences. Therefore, the design may have lacked sufficient sensitivity to reveal the performance effects of US recency.

There is, however, evidence for the role of non-associative performance effects in the priming variant of the Perruchet effect, also referred to as the reaction time (RT) version. In this version of the

design, participants are presented with a tone on every trial and the tone is followed by an outcome (white square) on half the trials, to which participants must make a button press response as quickly as possible. Response speeds to the outcome and expectancy for the outcome show opposite linear trends as a function of the preceding run type, with the fastest responses following a series of tone-outcome trials when expectancy for the outcome is lowest and the slowest responses following a series of tone-alone trials when expectancy for the outcome is highest (Perruchet et al., 2006). However, in a series of three experiments, Mitchell, Wardle, Lovibond, Weidemann, and Chang (2010) showed that the linear trend in reaction times was independent of the tone-outcome pairings. While there was an overall reaction time benefit for having the tone precede the outcome, the same linear trend in response speeds as a function of preceding runs was observed in a control group in which the outcome was presented alone, a control group in which the outcome preceded the tone, and a control group in which the tone and outcome were presented independently of each other. This evidence suggests that recency of the outcome (or recency of responding to the outcome) is the determinant of the linear trend in reaction time, and not recency of tone-outcome pairings (associative strength). While this conclusion is not universally accepted (e.g., Barrett & Livesey, 2010), it appears that non-associative factors might play an important role in the RT version of the Perruchet task. Whether the same is true of the Perruchet effect in other associative learning paradigms remains to be determined.

In a recent review of research on the Perruchet effect over the 30 years since he first introduced it, Perruchet (2015) concluded that the evidence still favors an explanation in terms of multiple learning processes. However he acknowledged that the most critical issue for the paradigm is “whether the behavioral effect may be thought of as the consequence of nonassociative processes, such as sensitization or arousal induced by E2”, where E2 refers to the outcome or US (Perruchet, 2015, p. 18). Accordingly, the present research pursued the approach of Weidemann et al. (2009) to further investigate the contribution of US-elicited non-associative processes to the CR trend in the eyeblink version of the Perruchet effect.

Each experiment sought to manipulate US recency while leaving the associative role of the reinforced and non-reinforced tone trials intact. One feature of eyeblink conditioning is that it is very sensitive to the temporal parameters between the CS and the US. Acquisition of the eyeblink CR is dependent on the CS preceding the US with a relatively short inter-stimulus interval (ISI; Joscelyn & Kehoe, 2005; Joscelyne & Kehoe, 2007; Smith, Coleman, & Gormezano, 1969). The present experiments take advantage of this temporal specificity by comparing the standard Perruchet design with a control group that receives the US even on “CS-alone” trials, but in such a way as to preserve the non-reinforced status of these trials from an associative learning perspective. Therefore, if associative strength determines the pattern of eyeblink CRs in the Perruchet design the same linear trend should be observed in the control group as in the standard Perruchet group. However, if US recency determines the pattern of eyeblink CRs then the linear trend should be reduced or eliminated in the control group. We did not record US expectancy ratings in these experiments because we were not seeking to demonstrate a dissociation between CRs and expectancy in the control conditions. Rather we used the control conditions to throw light on the mechanism underlying the CR trend in the standard Perruchet design.

2. Experiment 1

This experiment used a between-group design to assess the influence of associative and non-associative factors on CR pro-

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