

**Reward prediction error and declarative memory**

Kate Ergo<sup>1</sup>, Esther De Loof<sup>1</sup> & Tom Verguts<sup>1</sup>

<sup>1</sup> Department of Experimental Psychology, Ghent University, Henri Dunantlaan 2, B-9000  
Ghent, Belgium

*Correspondence:* [tom.verguts@ugent.be](mailto:tom.verguts@ugent.be)

Tom Verguts

Department of Experimental Psychology

Ghent University

Henri Dunantlaan 2, B-9000 Ghent, Belgium

Phone number: +3292646408



## Two Memory Systems, One Reward Prediction Error?

A tennis player knows how to perform a perfect serve, and also knows the opponent's name. But how are these two types of "knowing" similar, if at all? It is thought that the human brain houses at least two broad and distinct memory systems [1], each with its own learning algorithms and neural correlates. The first is **non-declarative** (or habit, or implicit) **memory** (Glossary). The second is **declarative** (or, in humans, propositional, or explicit) **memory**. The computational principle of **reward prediction error** (RPE)-based learning [2,3] is generally thought to drive non-declarative learning. We review recent evidence that RPEs also drive declarative memory.

One of the most influential theories in current cognitive neuroscience is predictive coding [4,5]. According to this account, the brain generates predictions about its own percepts, actions, and cognition, in order to learn about, build models of, and navigate the world [6]. A key concept in predictive coding is the **prediction error** (PE). Specifically, in order to generate accurate predictions, the brain needs to set a number of parameters (e.g., encoded in its synaptic connections). PEs allow updating such parameters.

Predictions can be made about several variables, such as tomorrow's weather, the next action I (or somebody else) will perform, our partner's mood, and so on. One particularly relevant variable to make predictions about, is reward; a PE in reward (by definition) is a RPE. The concept of RPEs has been very influential in non-declarative learning. In particular, RPEs were implemented in a wide range of computational models. For example, to account for blocking in non-declarative learning, Rescorla and Wagner (RW; [7]; Box 1) developed their now-classic model according to which learning depends on PE. Specifically, synaptic strength increases when a reward is better than expected, but synaptic strength decreases when the reward is worse than expected. Hence, the valence of the RPE matters (**signed** RPE) (SRPE). Further computational development of RW led to the temporal

difference (TD; Box 1) Reinforcement Learning model [3]. The TD model improved upon the RW model because it allows learning also when the reward is not immediately present. However, the main success of the RPE concept as implemented in TD was probably of an empirical nature. In particular, dopaminergic neurons in the ventral tegmental area (VTA) implement a TD-like RPE signature of reward processing [8,9]. In recent years, the role of TD-based RPEs in non-declarative learning has become well established in psychology, neuroscience, and Artificial Intelligence. For example, deep Reinforcement Learning models use TD-based RPEs to solve tasks (e.g., playing Atari games) that were long considered beyond the capacity of artificial agents [10,11]. In contrast to the RW and TD models that are SRPE based, Pearce and Hall proposed that learning occurs whenever reward is surprising (either better or worse, that is, different than expected; consistent with an **unsigned** RPE; Box 1) (URPE) [12]. It is noteworthy that normative, Bayesian models of learning exhibit features of both. For example, the Kalman filter [13] updates its estimates based on SRPEs, but its learning rate (i.e., the extent to which parameters (such as synaptic weights) are updated) is driven by uncertainty, which can be estimated via URPEs [14–16]. Empirical signatures of both SRPE and URPE have been observed in the brain [17].

### Reward Prediction Error in Declarative Learning

Although the role of RPEs in non-declarative learning has been studied extensively and formalized in a number of computational models, their role in declarative learning has only recently become a topic of interest. Two main approaches exist for elucidating the RPE effect on declarative learning (for an overview, see Table 1). First, in the *reward-prediction approach* (Box 2), a statistical distribution determines the probability of reward. The participant knows or estimates this reward distribution. Thus, the participant can make a prediction about reward; and based on the prediction, a RPE can be generated. Studies using

reward prediction can be approximately ordered based on the difficulty of this prediction, and we will discuss them in that order (easy to difficult). The study of [18] was one of the first to use such an approach. In an incidental memory task, each of three cues were linked to different reward values. A medium reward led to improved recognition when it was better than predicted (i.e., when it was preceded by a cue predicting low or medium reward) relative to when it was worse than predicted (i.e., preceded by a cue predicting high or medium reward), consistent with a SRPE effect. However, later work could not replicate the SRPE effect in this specific experimental paradigm [19,20].

A second implementation of the reward-prediction approach is the recent variable-choice paradigm (Figure 1a (Key Figure) and Box 2; [21]). Here, participants learn Dutch-Swahili word associations under different RPE value conditions. See Figure 1a for an overview of all RPEs in this design. Predicting the reward probability is again quite easy; participants can deduce it from the number of eligible options. Behaviourally, memory performance showed a SRPE effect in declarative learning: Recognition accuracy and certainty increased linearly with larger and more positive RPEs (Figure 1b). These results were replicated with image-word associations [21] and face-word associations [22].

In another instantiation of the reward-prediction approach, participants actively track and estimate the reward probability distribution. Here, on each trial, they experience a RPE relative to that (estimated) distribution (Figure 1c, Figure 1d and Box 2) [23–25]. Based on this feedback, they can update their estimate for subsequent trial estimates. For example, in [23], participants estimated the (fixed) probability of reward attached to specific stimuli. At reward feedback, a trial-novel image was presented. Subsequent memory performance for these trial-novel images displayed a SRPE effect, which was more pronounced in adolescents than in adults.

In [25], participants tracked the reward associated with different indoor and outdoor scenes. A clear URPE effect was observed: Scenes associated with a higher URPE during the initial task (i.e., with more surprising rewards, in either positive or negative direction), were afterwards better remembered (Figure 1c-d).

[26] used a reward-prediction paradigm to disentangle effects of SRPE, surprise (which corresponds to URPE), and uncertainty. Unlike in the other paradigms just discussed, reward probability was not fixed, but instead jumped to a different level at unpredictable time points in the experiment. Only SRPE had an effect on subsequent memory (Figure 1f) (see also [27]). Finally, in [24] the reward probability would fluctuate slowly but unpredictably on each trial, making the reward-prediction task very challenging. In this experiment, unlike the other discussed paradigms, a negative effect of (S)RPE was observed. Specifically, trials (and participants) with stronger and more positive RPEs, were associated with impaired declarative learning.

As a second approach, in a *multiple-repetition paradigm* (Box 2), a set of general information questions are repeated a number of times. Trial-specific confidence ratings (“How certain are you that you answered correctly?”) and feedback are used to compute trial-specific PEs. Given that being correct is rewarding [28], these PEs can be considered as RPEs. The researchers use these RPEs to predict accuracy on subsequent presentations of the same general information questions. Here, a URPE effect is typically observed. In particular, the hypercorrection effect obtained in this multiple-repetition paradigm entails that errors made with high confidence are beneficial for memory [29–33]. High-confidence errors are exactly those trials during which positive feedback was expected but not obtained; thus, this effect is consistent with a URPE effect. Also [34] observed a hypercorrection effect and interpreted it as a URPE. Additionally, in their experiment, participants received false feedback on a small fraction of trials (i.e., trials that were answered correctly but labeled as

false), and received novel feedback (i.e., a novel “correct” answer) on those trials. In those false-feedback trials, a URPE effect was also observed: On trials that were answered with high certainty but that were not rewarded (high URPE), the novel feedback was subsequently recalled more confidently.

Overviewing and categorizing these paradigms, we note that a main difference between the reward-prediction and multiple-repetition approaches is the origin of the RPE: An independent reward generation mechanism in the former, and the participant’s own confidence in his or her memory in the latter. Another difference is that, in the reward-prediction approach, RPEs are usually computed or estimated, whereas RPEs are deduced from confidence measures in the multiple-repetition approach. There are some exceptions to the latter rule: For example, [25] implemented a reward-prediction paradigm where confidence is used to calculate a RPE. Finally, in the reward-prediction paradigm, memoranda are usually trial-unique, whereas (by definition) they are not in the multiple-repetition approach. These are just a few of the relevant dimensions; we discuss some other potentially relevant dimensions in the next section.

## Open Issues

Despite the recent interest and steeply growing data set on RPEs that drive declarative memory, many uncertainties remain. We discuss a few of them in the next paragraphs.

### **RPE: Signed or Unsigned?**

Studies with a multiple-repetition paradigm typically observed URPE (i.e., surprise) effects. Instead, the reward-prediction paradigm has tended to yield SRPE effects. But also URPE effects have been documented with a reward-prediction paradigm (Figure 1d) [25]. Why do different designs generate SRPE versus URPE effects on declarative learning? One

potentially relevant factor is the range of the RPEs probed. In particular, studies that found a behavioral SRPE effect (i.e., most reward-prediction paradigms) might simply not have investigated the full range of RPEs. In the variable-choice paradigm [21,35], this could be tested by including a few non-rewarded one-option (high-certainty) trials. These highly infrequent events would be accompanied by large negative RPEs.

However, this is unlikely to be the full story, because both RPE signatures have been observed even within a single study. In an EEG study with the variable-choice paradigm [35], an URPE pattern was observed during reward feedback in the theta (4-8 Hz) frequency band, consistent with literature implying theta in URPE processing [36]. Instead, SRPE signatures were found in the high-beta (20-30 Hz) and high-alpha (10-15 Hz) frequency ranges, consistent with a functional role of both beta and alpha power in reward feedback processing [37,38]. Furthermore, in an fMRI study using a multiple-repetition paradigm, [34] found SRPE-consistent activation in several areas (including striatum), but URPE signatures in others (including insula). Together, these findings suggest that both SRPE and URPE are important for declarative learning; and that we need an account identifying the functional role of each, in time, (neural) space, and frequency band. The Bayesian learning model mentioned in the introduction, which naturally incorporates both, may be a useful starting point in this respect.

### Timing Issues of RPEs

In most paradigms, a novel declarative memorandum is presented on each trial, followed by a RPE, followed by declarative feedback about what the correct answer should have been (see Figure 1a, word pair encoding for an example). Here, RPE can have either a retrograde effect (if it interacts with the originally presented memoranda), or instead an anterograde effect (if it interacts with the declarative feedback). Concerning the anterograde



effect, in the variable-choice paradigm, the declarative feedback appeared either simultaneously with the RPE (delay of 0 ms; [21]), or with a delay of 3000 ms [35]. The fact that we find very similar results in the two cases suggests that the timing of the RPE-feedback interval is not very crucial, at least within the first few 100s of ms. An interesting parallel can be drawn here with the test-potentiated learning effect from the declarative memory literature. Here, taking a test potentiates the learning of (old or novel) material that is subsequently presented [39,40]. Also for a retrograde effect (of RPE on originally presented memorandum), an interesting analogy can be made with earlier literature. In particular, [41] found a retrograde effect of reward on declarative memory, with objects that were (temporarily) closer to (subsequent) reward being better remembered afterwards. In the reward-prediction approach, it remains to be shown which of these two (anterograde or retrograde effect of RPE) is crucial for driving the RPE-based declarative memory improvement.

A RPE can also appear at cue rather than at feedback. The only paper thus far investigating both cue- and feedback-locked RPE effects is [26]. These authors observed cue- but not feedback-locked RPE effects; however, in their experiment, there was both a cue- and a feedback-locked RPE on each trial. It is very well possible that an initial RPE suppresses a second RPE occurring (e.g., a few 100 ms later) in that same trial. We conclude that RPE timing issues need to be studied more systematically. In particular, if this research is to have practical application in education, such studies will be imperative.

## **RPE: Why and How?**

In non-declarative learning, a normative argument for *why* to use RPE is well established: Calculating RPE is necessary for online (i.e., while interacting with the world) reward maximization [3]; this idea is inherent in the RW, TD, and Pearce-Hall models (Box

1). Does this argument apply to declarative memory as well? An intuitive argument is that it makes sense to only remember stimuli (or more generally, episodes) that are associated with a reward level that is sufficiently different from what is already expected. Indeed, if a stimulus from some category is accompanied by reward each time it is encountered, it makes little sense to explicitly remember each novel stimulus instance as a separate event once it has already been learned.

Another issue is *how* RPE improves memory. One potential mechanism is via phase-locking to neural oscillations in specific frequency bands. In particular, neural **theta phase synchronization** may provide one (but not exclusive) solution: Brain areas in theta phase synchrony are thought to communicate and learn more efficiently [42], thus facilitating memory integration [43]. Indeed, episodic memory is enhanced when multimodal (audio-visual) stimuli are synchronously presented in theta phase; with stronger theta phase synchronization predicting better memory performance [44,45]. Dopaminergic midbrain neurons have also been found to phase-lock to (cortical) theta during encoding, with stronger phase-locking during subsequently remembered (versus forgotten) memoranda [46]. Thus, it is possible that RPEs (via neuromodulatory signaling) increase theta synchrony, which subsequently allows the relevant brain areas to “glue” the episode together more efficiently [47]. The EEG variable-choice paradigm study mentioned above [35] provides preliminary evidence for this view. Further, computational models that consider RPE-theta interactions to drive learning, have started to appear [48].

Whereas dopaminergic RPEs likely support non-declarative learning via basal ganglia pathways, dopaminergic RPEs may support declarative memory via hippocampus [49]. Standard theory holds that (dopaminergic) VTA calculates SRPE, but a substantial number of URPE neurons have also been observed in VTA and nearby midbrain areas [50]. Moreover, also noradrenergic locus coeruleus projects to hippocampus and may thus exert URPE effects

[51]. Earlier authors proposed that VTA-hippocampus interactions originate in hippocampus [52]. We propose that VTA-hippocampus interactions may also originate in VTA, and that SRPEs (encoded by VTA, possibly based on input from ventral striatum; [53]) and URPEs (encoded in VTA and locus coeruleus) may modulate hippocampus for episodic memory encoding. Consistently, a number of studies have demonstrated that midbrain VTA activation (triggered by reward or by RPE) is associated with improved episodic learning [22,54,55].

### **The Effect of Test Delay on Declarative Memory**

In declarative memory studies, participants are typically subjected to an implicit or explicit memory test; either on the same day or after a considerable delay (ranging from a few hours to a few weeks). If, as suggested above, SRPEs are encoded by dopamine neurons, then effects should be stronger with longer delays. Indeed, although early and late long-term memory effects both rely on dopamine, late effects have a stronger dependency on dopamine [49]. Consistently, an effect of reward in declarative learning is typically stronger after a delay [56,57]. However, a systematic comparison of the delay-by-RPE interaction on declarative memory remains to be carried out.

### **Reconsolidation**

When information is retrieved from memory, it enters a plastic, labile state, allowing the information to be changed, strengthened or weakened, a process called reconsolidation [58,59]. This finding is most intensively studied in non-declarative memory [60], but is observed in declarative memory as well [61]. PE is required for reconsolidation [62] both in non-declarative [63] and in declarative memory [61,64]. Given the important role of RPE in declarative learning, and given that similar principles drive learning and reconsolidation [64], we predict that RPE may modulate reconsolidation too. The multiple-repetition approach,

where declarative memory is probed iteratively, can be considered as a first attempt at investigating RPEs in the context of reconsolidation. This remains, however, to be further investigated.

## Concluding Remarks and Future Perspectives

Learning, RPEs, and declarative memory are sometimes treated as separate topics, each with their own prominent paradigms, findings, and theories. The current perspective suggests instead that they are intimately related. Briefly, learning is modulated by RPEs, and leads to (declarative) memory traces in the brain. We discussed a few recent paradigms that started to explore such interactions. In the Open Issues section, we highlighted a number of dimensions of those paradigms, that if addressed, could greatly facilitate further development of the research field. Although much remains to be found out, concrete models and predictions are beginning to emerge, with relevance for both Natural and Artificial Intelligence. We are excited about what the (near) future will bring in that respect, not only because of its conceptual unification, but also because of its promise for informing educational policy and practice.

## Glossary

**Declarative memory:** Memory for facts and events (“knowing what”), that can (at least in humans) be (consciously) declared; it is typically considered to consist of episodic memory (memory for single episodes) and semantic memory (memory for information aggregated across several episodes). The process of acquisition of declarative memory is called declarative learning. Encoding declarative memories can happen rapidly, typically after only a single exposure (for both episodes and semantic content), and relies heavily on the hippocampus [65].

**Non-declarative memory:** Non-declarative learning is an umbrella term for the acquisition of different types of knowledge, including procedural memory (“knowing how”). This involves acquiring a motor or cognitive skill (procedure) by means of repeated practice (e.g., learning to play tennis).

**Prediction error:** Difference between the actual value of some variable and predicted value of that variable (i.e., actual value minus predicted value).

**Reward prediction error:** Prediction error where the relevant variable is reward (i.e., actual reward – predicted reward). See also **Prediction error**.

**Signed:** In mathematics, signed means that the sign of a number is taken into consideration (e.g., -3, +3). In the context of SRPEs it indicates that we take the valence (positive versus negative RPEs) into account.

**Theta phase synchronization:** Synchronization of two brain areas in the theta frequency (4-8 Hz). Such synchronization can be achieved by making the theta phase of the two areas identical, so that theta waves in both areas “go up and down” together.

**Unsigned:** Unsigned means that the sign is not considered (i.e., absolute value is taken, e.g., -3 and +3 both have an unsigned value of 3). See also **Signed**.

### Box 1. Models of Learning

The *Rescorla-Wagner model* [7] describes learning the value (expected reward) of specific events (say, events A and B). This information is encoded in their associative strength to a “value” unit, symbolized as  $w_A$  and  $w_B$  for events A and B, respectively. Specifically, based on whether events A and B occur ( $x_A = 1$  and  $x_B = 1$ , respectively) or not ( $x_A = 0$  and  $x_B = 0$ , respectively), an additive prediction is made about the occurrence of reward ( $V = x_A \times w_A + x_B \times w_B$ ). When reward finally occurs (or not), a reward prediction error is calculated ( $R - V$ ), where occurrence of reward (denoted  $R$ ) is typically coded as  $R = 0$  (when there is no reward)

or  $R = 1$  (when there is reward). This reward prediction error is then used to change the connection strength between cells encoding A and B on the one hand, and reward on the other:  $\Delta w_i = \alpha \times x_i \times (R - V)$ , with  $i \in \{A, B\}$ . After repeated application of this learning rule, the weights  $w_A$  and  $w_B$  allow the model to accurately predict reward, based on the (A, B) input combination.

*Temporal Difference model* [3]. The Rescorla-Wagner model can only learn from external feedback ( $R - V$ ). This is computationally inefficient because reward may be not delivered at each time point where relevant information is provided to the organism. In temporal difference learning, learning can also occur if the *prediction* of reward changes between two time points  $t$  and  $t + 1$ . Formally, the learning rule becomes (now with explicit time index  $t$ ):  $\Delta w_i(t) = \alpha \times x_i(t) \times (R(t) + \gamma V(t + 1) - V(t))$ , with  $i \in \{A, B\}$ . If  $\gamma = 0$ , the rule reduces to the Rescorla-Wagner rule. In case  $\gamma > 0$ , learning can also proceed at times  $t$  where no actual reward was delivered, rendering the algorithm more powerful than the Rescorla-Wagner rule.

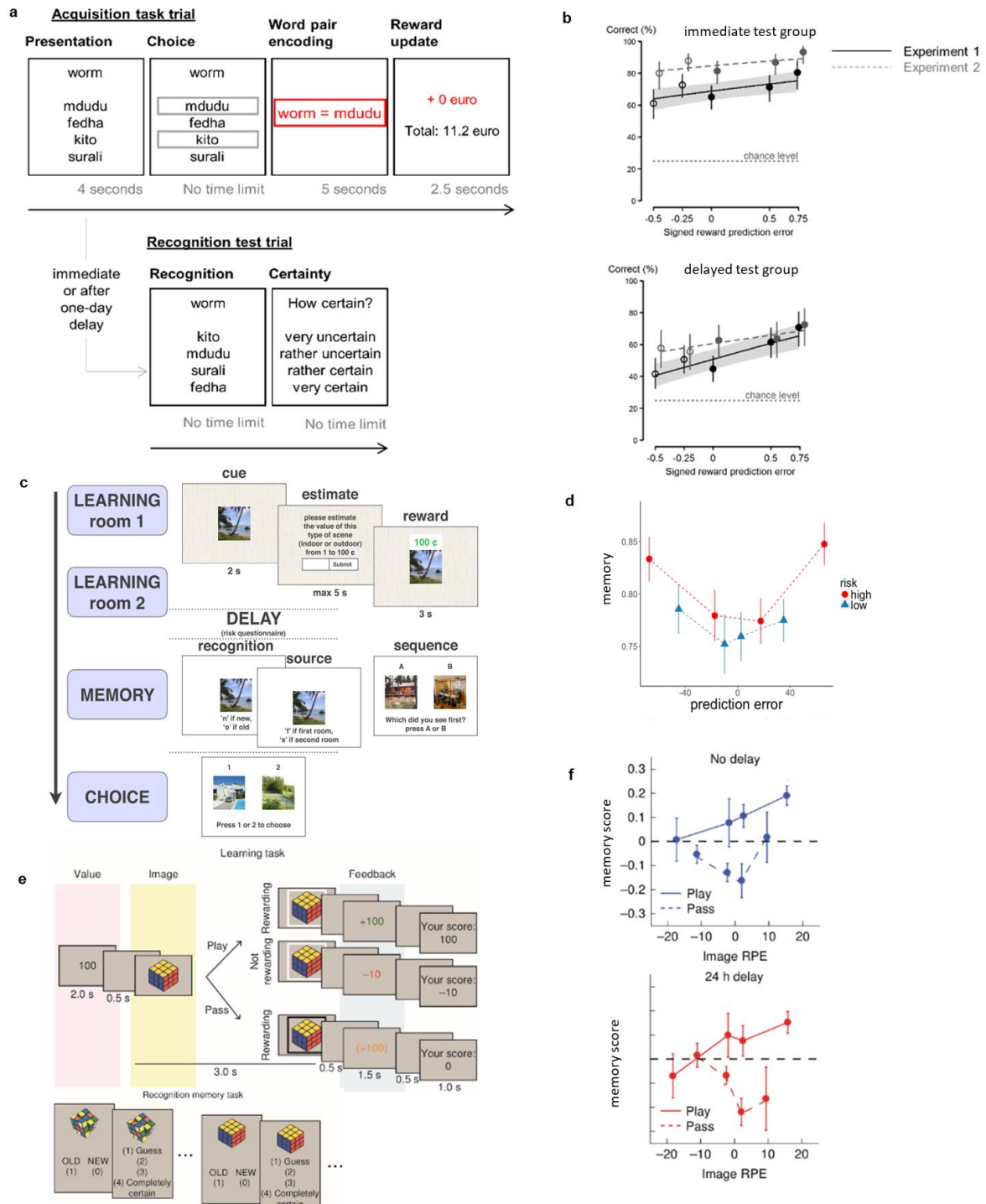
*Pearce-Hall model*. According to this model [12], learning only occurs when a reward is surprising. Specifically, it uses the absolute value of a RPE (“different than expected” signal), consistent with an unsigned RPE approach. Formally, (one variant of) the learning rule can be written as:  $\Delta w_i(t) = x_i(t) \times R(t) \times |R(t) - V(t)|$ .

## **Box 2. How to Generate and Measure RPEs: Experimental Approaches**

*Reward-prediction approach*: Here, participants must both learn declarative information (e.g., word pairs) and simultaneously estimate a (potentially non-stationary) reward distribution throughout the task [24–26]. In some cases, the correct RPE can be easily derived analytically; in other cases, RPE can only be calculated after fitting a reinforcement learning

model, and deriving the RPEs from the model estimates [24,26]. One example of a reward-prediction approach is the variable-choice paradigm. In the variable-choice paradigm [21,35] (Figure 1a), participants learn stimulus pairs, such as Dutch-Swahili word pairs or image – Swahili stimulus pairs [21]. In the former example, on each trial, a Dutch word is shown together with four Swahili words. Critically, the number of eligible options is manipulated. In the one-option, two-option, and four-option conditions, one, two, or four Swahili words are eligible (framed), respectively; and the probability of choosing the correct translation is thus 100%, 50%, or 25%, respectively. Feedback is given on every trial. Signed and unsigned trial-by-trial RPEs are calculated based on the difference between actual and predicted reward (see Glossary). Memory is probed in a subsequent recognition test.

*Multiple-repetition approach:* Here, general information questions are repeatedly presented, and a RPE is estimated based on previous presentations of each question. For example, in [34], participants first studied a text, and subsequently received (multiple-choice) questions about the text. After each question, they rated confidence and received feedback. The trial-by-trial PE was calculated using the confidence rating and feedback. Hypercorrection effect studies also typically use a multiple-repetition paradigm [31,66].



## Figure Captions

**Figure 1.** RPE in declarative memory: Reward-prediction approach applied in three paradigms and typical findings. a) Variable-choice paradigm and design from [21]. b) Variable-choice paradigm behavioural results show a SRPE signature for recognition in both the immediate and delayed test group; recognition of word pairs increased linearly with larger



357 and more positive RPEs. c) Paradigm reproduced from [25]. d) [25] found a URPE (U-  
358 shaped) signature; with memory improving for both large negative and large positive RPEs.  
359 e) Paradigm reproduced from [26]. f) Jang et al. (2019) found a SRPE signature: Memory  
360 score increased with increasing RPE.

361

362 **Table 1.** Non-exhaustive overview of studies on RPE in declarative memory.

Authors	Approach	Task & Stimuli	SRPE/ URPE	Effect on memory
<b>Bunzeck et al. (2010)</b>	Reward prediction	Each of three cues (colored squares) is followed by one of two potential reward values (medium-low, medium-high, and low-high), so a medium reward can be better or worse than expected. After reward feedback, a novel (indoor or outdoor) scene is presented. Scene recognition is probed after a one-day delay.	SRPE	Positive
<b>De Loof et al. (2018)</b> (see also Figure 1a-b)	Reward prediction	On each trial, participants see one Dutch word together with four (trial-novel) Swahili words and choose a translation from either one, two or four of these Swahili words. Manipulating the number of eligible options (1, 2, or 4) and whether a trial is rewarded or not, allowed manipulation of RPEs. For example, in the case of a four-option, rewarded trial, participants experience a RPE of $1 - \frac{1}{4} = .75$ ; in case of a two-option, non-rewarded trial, participants exhibit a RPE of $0 - \frac{1}{2} = -.50$ .	SRPE	Positive
<b>Davidow et al. (2016)</b>	Reward prediction	A cue is presented with two targets linked to different reward values. Subjects must (learn to predict and) choose the high-value target. Trial-novel images are shown during subsequent reward feedback. Image memory is probed afterwards via old/new judgements.	SRPE	Positive
<b>Rouhani et al. (2018)</b> (see also Figure 1c-d)	Reward prediction	Participants track the reward associated with different indoor and outdoor scenes. On each trial, participants predict the reward (for a particular scene), and subsequently receive feedback about their estimate. From this difference (feedback - predicted reward), a	URPE	Positive

<b>Jang et al. (2019)</b> (see also Figure 1e-f)	Reward prediction	RPE can be calculated. Scene memory is probed after this initial task via old/new judgments.	SRPE	Positive
		On each trial, participants see a value and a stimulus (animate or inanimate) for that trial, and decide to play or pass on that trial (Figure 1e). After each choice, the image is shown with reward feedback. Afterwards, recognition memory for the images is probed via old/new judgements.		
<b>Wimmer et al. (2014)</b>	Reward prediction	Participants track the drifting reward probability of colored squares, which are overlaid with incidental trial-unique images and followed by feedback. Recognition memory for the images is probed via old/new judgements after a one-day delay.	SRPE	Negative
<b>Butterfield &amp; Metcalfe (2001)</b>	Multiple repetition	Participants are presented with questions for which they have to generate an answer and rate their confidence, followed by a surprise retest.	URPE	Positive
<b>Metcalfe et al. (2012)</b>	Multiple repetition	Participants are presented with general information questions. In a first test phase, participants provide answers and rate their confidence. In the subsequent phase, subjects received feedback about their answers. Finally, participants are retested on a subset of questions in a second test phase.	URPE	Positive
<b>Pine et al. (2018)</b>	Multiple repetition	Participants study a text and are tested after two days, at which time they also provide confidence ratings for their answers. On a small fraction of trials, participants receive false feedback (i.e., trials that were answered correctly but labeled as false), and received novel feedback (i.e., a novel “correct” answer)	URPE	Positive

on those trials. A second (incidental) test is given after 7 days.

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