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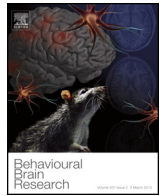
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Research report

An associative analysis of object memory

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HIGHLIGHTS

- Synopsis given of model of associative memory whose origin is as a theory of Pavlovian conditioning.
- Object recognition tasks are explicable in terms of the associative memory model.
- Experimental predictions from the associative model are found to be supported.

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ABSTRACT

Different aspects of recognition memory in rodents are commonly assessed using variants of the *spontaneous object recognition* procedure in which animals explore objects that differ in terms of their novelty, recency, or where they have previously been presented. The present article describes three standard variants of this procedure, and outlines a theory of associative learning, SOP [1] which can offer an explanation of performance on all three types of task. The implications of this for theoretical interpretations of recognition memory and the procedures used to explore it are discussed.

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1. Introduction

We may take recognition memory as being the discrimination between novel and familiar events [2–4]. It has been popular to examine recognition memory in rodents by capitalising on their tendency to approach and explore novel or unexpected objects in preference to familiar or expected objects [5,6]. Systematic variations in this procedure have encouraged particular accounts of the psychological processes underlying object recognition: Ennaceur & Delacour [7] (see also [8,9]) parsimoniously describe memory as the habituation of an approach response towards an object with increased exposure; Aggleton and Brown [10] maintain that it is

based on a sense of familiarity towards an object that is built up through exposure to it (see also [2,11]); Cowell, Bussey, and Saksida [12] describe a multi-layer connectionist network that allows recognition to occur as in the natural course of the building of stimulus representations and several authors have suggested that rodents' recognition memory represents a relatively sophisticated form of mnemonic process [13,14].

In this report we describe an alternative psychological account of recognition memory, which is based on Brandon, Vogel, & Wagner's model [15], SOP (Standard Operating Procedures; [16–18]). SOP is primarily a model of associative learning, but unlike some others [19] incorporates a conceptualisation of memory. We argue here that this feature of SOP allows it to accommodate much of what is known about rodents' object recognition and show that it has generated predictions that have been experimentally supported. SOP has produced successful accounts of many phenomena (e.g., habituation [3,20,21], associative learning, discrimination learning) and if its account of object recognition were accepted, it would strengthen its position as a general-purpose model of adaptive behaviour.

Abbreviations: A1, primary state of stimulus element activity in SOP; A2, primed or secondary state of activity in SOP; CS, conditioned stimulus or signal; US, unconditioned stimulus or outcome.

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		Preexposure 1	Preexposure 2	Approach bias on test
Type of object recognition	Spontaneous object recognition	P	-	$P < Q$
	Relative recency	P	Q	$P > Q$
	Object in context	xP and yQ	-	$xP < xQ$

Fig. 1. Object recognition experimental designs. Experimental designs for three, key types of object recognition procedure: spontaneous object recognition, relative recency and object-in-context. P and Q refer to distinctly different objects; x and y refer to distinctly different contexts. The inequality signs indicate the object that elicits the most approach behaviour.

2. Object recognition in non-human animals

2.1. General procedural features and experimental considerations

Spontaneous object recognition [7,22–25], relative recency [13,26–31] and object-in-context [32–38] are terms given to three of the most popular procedures for looking at object memory in rodents (see Fig. 1). We describe each in turn, before discussing an associative model of memory, SOP, [15] that can provide a satisfactory explanation of performance on these three tasks, and also generate novel, testable predictions.

All three procedures involve the placement of a rodent in one or more experimental contexts along with one or more objects; unlike matching- and non-matching-to-sample procedures for studying memory [39–41], food reinforcement is not used in these tasks. Experimental contexts vary in complexity, from being a single undecorated wooden box to pairs of contexts differentiated in their floors and/or walls. The experimental objects are often domestic items (bottles, vases, etc.) that are selected to be difficult for rodents to knock over, chew or sit upon, behaviours that could easily contaminate the measured behaviour. The three tasks differ principally in the preexposure that rodents receive (which is fully described below). For example, in spontaneous object recognition one object, P, is preexposed. In all three tasks, test performance involves the simultaneous presentation of a pair of different objects (P and Q), which have been treated differently earlier in the procedure (but see [42]). The experimenter will measure differences in the amounts of behaviour directed towards objects P and Q. This may either be specific exploratory responses [32,33] or entry into notional zones that surround each object [31,43,44]. In spontaneous object recognition, approach to P is depressed relative to Q on test [26,33] and decreases over the course of pre-exposure [20,45].

Interpretation of a difference in behaviour towards objects P and Q requires appropriate experimental management. For example, it is essential to counterbalance the objects serving as P and Q (e.g., half of the rodents have a bottle as P and a vase as Q; the remaining rodents receive the reverse arrangement) as well as their positions within the context (e.g., half of the rodents receive object P on the left of object Q; the remaining rodents receive the reverse arrangement). It is also necessary to ensure that the two objects do not differ in their marking (e.g., by odour cues), which may be achieved either by cleaning or replacing them after use.

2.2. Three types of object recognition task

In a *spontaneous object recognition* experiment [7,22–25], rodents receive a pre-exposure trial with object P before testing with P and a novel object, Q. Q is approached in preference to P on

testing. Typically two versions of a single object (here, P) are pre-exposed so that the arrangement of objects in the context during preexposure matches that during testing. Just as in delayed non-matching to sample [46–49], in spontaneous object recognition the interval between pre-exposure and testing can be extended to reduce test discrimination [50–52].

This temporal dynamic of the interval between preexposure and test is explicitly manipulated in the *relative recency* procedure [13,26–31]. Here two pre-exposure trials precede testing: the first is with P; the second with Q. On test, rodents approach P more than Q, demonstrating better memory of the more recently presented Q. The interval between the two pre-exposure trials and the interval between the second pre-exposure trial and test will emerge later as important considerations in the evaluation of the associative analysis of object memory.

Like the relative recency procedure, the *object-in-context* procedure involves the separate pre-exposure of both objects P and Q before the test. The difference is that pre-exposure to each object occurs in a distinctly different context: Object P in context x and object Q in context y. Greater approach towards Q than P is found when testing occurs in context x [32–38]; and, of course, testing may be given in context y in which approach is biased towards P. The particular sequence of pre-exposure trials (xP before yQ or the reverse) may constitute a relative recency manipulation and its implications for our evaluation of SOP are considered below (Section 3.4.3).

2.3. Brain areas associated with these three types of object recognition

Although our report is intended to consider a psychological-level of analysis of recognition memory it is worthwhile to consider brain areas that are associated with the three forms of object recognition. Evidence of the importance of the perirhinal cortex in spontaneous object recognition is excellent in that there are many examples of its involvement (primarily from lesion studies in rats) from a variety of labs (e.g., [22,23,28,37,45,49,53,54]) and, as far as we are aware, there are no claims of null findings. There is also some evidence of involvement of prefrontal cortical regions [28] but mixed findings of involvement of the hippocampus (e.g., with deficits reported in some labs, e.g., [23,50], but not in others, e.g., [35,38,55]). Fewer brain regions have been examined in relative recency procedures but there is abundant evidence for the involvement of specific regions of the prefrontal cortex in rats (e.g., [27,28,56,13,57]) and, again of the perirhinal cortex and its connections with the prefrontal cortex (e.g., [28,13]). Object-in-context learning has been demonstrated to be affected by manipulations of the hippocampus (e.g., [35,38,55], see also [58] for evidence of hippocampal involvement in an audio-visual analogue of object-in-context learning) and the prefrontal cortex (e.g., [28,36]).

3. The SOP model of associative memory

3.1. Stimulus representation

According to Brandon et al.'s SOP model, all stimuli are represented by populations of stimulus elements that code for the perception and memory of physical characteristics. Because such elements may only be present or absent on a trial they constitute a binary code capable of describing a stimulus. For example, a pure tone presented to a rat might have elements of a 2.0-kHz pitch and a 65-dB (SPL) amplitude. This is, of course, a simplification—many more stimulus characteristics will be available for coding—but it is sufficient for this explanation. Through learning—for example, pairing the tone with delivery of food—the elements comprising the

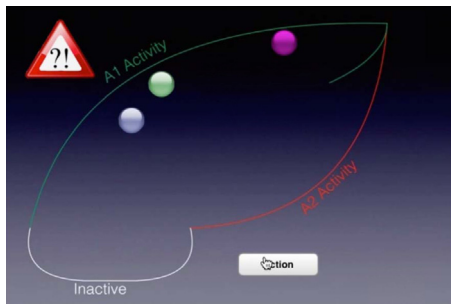


Fig. 2. Activity transitions of stimulus elements.

This figure is a still from a movie that is embedded in the PDF version of this manuscript (see Appendix A). The movie represents the sequence of activity transition states in Brandon et al.’s SOP model. Three stimulus elements are initially in an inactive state. Clicking the “Activate” button is analogous to the presentation of a stimulus to an organism, such as the presentation of a tone to a rat. The rat will typically show a strong orienting response to the source of the tone (represented as, “?!”), corresponding to the stimulus elements’ promotion to their A1 states of activity. The elements are next “primed” (i.e., they enter an inferior A2 state of activity) where they provoke weaker orienting responses. Finally, the elements re-enter their inactive states where they do not provoke stimulus-specific behaviour. For computational reasons, Brandon et al. conceive of stimulus representations as comprising much larger populations of elements than this; nonetheless the sequence in which the stimulus elements pass through the various activation states is identical, and elements cannot pass directly from A2 back to A1. Thus presentation of the tone (i.e., clicking “Activate”) when its elements are in their A2 state does not promote them into their A1 state: Entry into A1 state must come directly from the inactive state.

tone representation would become associated with the representational elements that code for the food (with their own distinctive coding properties relating to its smell, texture, etc.) Presentation of the tone could produce food-related responding by activation of the food stimulus elements via these inter-element associations. Moreover, presentation of a physically similar, but discriminably different, tone (e.g., one having a 1.8 Hz pitch with an amplitude, again, of 65 dB SPL) could also produce responding, albeit at a reduced level, to the extent that it shared one or more stimulus elements with the tone used in training [59–61].

3.2. Activity states, their transitions and behaviour

Hebb [62] described learning principles in which cell assemblies (which are notionally identical to stimulus elements in SOP) are in either active or inactive states. Coincident periods of activity in cell assemblies would promote the formation of excitatory associations. However, Hebb’s system fails to predict hallmark associative learning phenomena such as blocking and relative validity [63,64]. Like Hebb’s model, SOP supposes that concurrently active stimulus elements will support association formation (this will be outlined below in Section 3.3) but supposes the existence of two qualitatively different forms of activity.

A representation of a brief, 2.0-kHz tone’s stimulus elements and their transition through SOP’s activity states is summarised in the HTML movie in Fig. 2. The tone’s elements begin in the inactive state and they will not elicit any behaviour. Clicking the Action button corresponds to the presentation of the tone and this will promote the tone’s elements into their primary form of activity (A1 state) in which they will elicit behaviour. On initial presentation of a tone, the rat will elicit a strong orienting response [9], for example towards the loudspeaker and this is represented by the large hazard sign, marked with “?!”. With sustained or repeated presentation, the tone’s elements will fade into their secondary state of activity (A2 state) where they will elicit weaker orienting, which is represented by a smaller hazard sign marked with “?”. Elements in their A2 states are referred to as *primed*. After their period of A2 activity, or priming, the elements decay to their inactive states and no longer elicit orienting. Three points are notable here: 1. The momentary

probability of each element’s transition from one state to the next need not be uniform. This allows elements of a single stimulus to inhabit different activity states at the same time; 2. A stimulus element is assumed to be indivisible—it cannot inhabit more than one activity state simultaneously; 3. Elements must pass into their A1 states via their inactive states, as we saw in the movie: They cannot move directly from A2 to A1. Thus, for example, a second presentation of the tone while the elements are in their A2 states does not return them to their A1 states.

Brandon et al. describe a second, associative route of priming in SOP. Following successful associative learning, for example in an appetitive conditioning procedure, a tone signal will generate A2 activity in the food outcome. That is, the presentation of the tone generates A1 activity in its central representation, which primes the food’s representation directly into the A2 state via the excitatory association between them. Once primed, the food representation provokes conditioned responding. SOP’s associative priming allows it to accommodate many long-standing phenomena in animal discrimination learning, such as blocking [64,65] and relative validity [63] – in keeping with other models [19,60,66]. Associative priming also allows SOP to correctly anticipate that associative learning will reach an asymptote, a feature lacking in Hebb’s [62] model.

3.3. SOP’s rules for association formation

Having outlined SOP’s transition characteristics for stimulus elements we are in the position to understand its four rules for associative learning. The rules are straightforward and represented in Fig. 3: Excitatory associations will be formed between stimulus elements whose elements are simultaneously in their A1 states (first rule); inhibitory associations will be formed from A1-state

Signal (Tone) (or Context)	Outcome (Food) (or Object)	Signal → Outcome Association Change	Examples
A1	A1	Excitatory	<i>Pavlovian conditioning:</i> Tone → Food
A1	A2	Inhibitory	<i>Feature-negative discrimination:</i> Light → Food & [Tone + Light] → No Food <i>Backward Pavlovian conditioning:</i> Food → Tone
A2	A1	No learning	-
A2	A2	No learning	-

Fig. 3. SOP’s rules for association change. According to the SOP model (e.g., Brandon et al., [11]) stimulus representational elements may exist in two states of activity, A1 or A2 (or in an inactive state, which is not represented here). When stimuli, or more precisely, their elements, are active together, changes in associative strength may occur. For example, the pairing of a tone and food delivery in an appetitive conditioning experiment with rats will encourage excitatory changes in association (“→”), which will promote the conditioned response. Early in training the tone and the food will tend to be in their A1 states. Learning will reach asymptote (its maximum level) because the tone’s excitatory association will prime the food into its A2 state generating a portion of inhibitory strength change. Changes in excitation and inhibition will balance at the asymptote. In *feature-negative discriminations* (also known as Pavlovian conditioned inhibition) a light might first be established as a signal for food. Later, the light may be presented in compound with a tone but with no subsequent food reinforcement. During these trials, the tone’s elements will largely be in their A1 states and the food’s elements will be in their A2 states, having been associatively primed by the light. The co-occurrence of the tone’s A1 and the food’s A2 states, produces the conditions necessary for the formation of tone-food inhibition. In *backward conditioning* the arrangement of the tone and food is reversed from that of standard Pavlovian conditioning—the food is presented just before the tone. This arrangement will produce inhibition by decay-based priming because the food’s representational elements may decay into their A2 states by the time of the tone’s presentation – thus arranging, again for the co-occurrence of the A1-tone and A2-food activity necessary to foster tone-food inhibition. In the application of SOP to object-in-context learning, the object may be conceived of as analogous to the food and the context, analogous to the tone.

elements to A2-state elements (second rule) but no associations will be reciprocated (third rule). No associative changes will occur among A2-state elements (fourth rule). Future presentations of a stimulus will activate the representation of associated elements via excitatory associations into their A2 state; but inhibitory associations will prevent this, leaving the elements inactive. We next outline circumstances in Pavlovian conditioned experiments where SOP assumes these associative changes take place.

In standard Pavlovian conditioning in which, for example, rodents receive a brief tone whose termination is coincidental with delivery of a food pellet (Tone \rightarrow Food; e.g., [67,68]), the pairing of the tone and food will tend to promote their stimulus elements into their A1 states and this will support excitatory conditioning. SOP predicts that the best condition for supporting associative change is when stimulus elements are paired *simultaneously* but Pavlovian conditioning procedures typically involves the *serial* pairing of the signal (or conditioned stimulus – CS) and outcome (or unconditioned stimulus – US). The reasons for this are merely practical: With serial signal \rightarrow outcome pairings, measurement of responding to the CS is free of contamination from the unconditioned responses to the outcome. However, specially designed analytical experiments have found learning about simultaneously presented stimuli to be superior to learning about serially presented stimuli [69], the finding anticipated by SOP.

An inhibitory signal for an outcome (an inhibitor) will not produce distinct behaviour when tested directly in the way that an excitatory signal will. Instead, inhibition is inferred from the results of a pair of indirect tests for inhibition [70]. In “retardation tests”, the inhibitor serves as a standard Pavlovian signal for the outcome following inhibition training. The acquisition of (excitatory) conditioned responding to the inhibitor is slow relative to an appropriate control condition. The “summation test” involves the superimposition of the inhibitor on a previously established excitor for the same outcome. The inhibitor reduces the conditioned response that is otherwise elicited by the excitor. Retardation and summation tests complement each other and many argue that both must be passed to claim that a stimulus is a true inhibitor [71].

“Backward conditioning” and “feature negative training” procedures have both been found to produce inhibition by retardation and summation testing. A1-signal activity can be paired with A2-outcome activity in Pavlovian conditioning when the “outcome” precedes, rather than follows, the “signal” (i.e., outcome \rightarrow signal pairings, or “backward conditioning”). When tested after training the signal may produce negligible performance [72], which SOP would assume to be the result of a mixture of excitatory and inhibitory signal–outcome learning caused by the A1-signal activity’s co-occurrence with the outcome’s elements as they decay from A1 to A2 activity states. With alterations in experimental parameters, it is possible for outcome \rightarrow signal pairings to produce full inhibitory learning in which the signal is found on test to suppress activity in the outcome representation [72]. Here SOP will assume that there is greater co-occurrence of the outcome’s A2 state and the signal’s A1 state than the outcome’s A1 state and the signal’s A1 state. A commoner method for arranging the pairing of A1-signal and A2-outcome activity is feature-negative discrimination training [70,71,73]. Here some third stimulus, e.g., a light, is established as a signal for food and the tone and light are presented as a compound, which is not reinforced by food delivery (i.e. Light \rightarrow Food, [Tone + Light] \rightarrow nothing).

There are important parallels between SOP and its better-known relative, the Rescorla and Wagner model [19]. The Rescorla and Wagner model describes the notional changes in associative strength between the representations of a pair of events on any particular trial, by the expression, $\Delta V = \alpha\beta(\lambda - \Sigma V)$. In particular, the change in associative strength (ΔV) is proportional to the difference in the maximum level of associative strength

(asymptote, λ) and the sum total of each previous associative change (ΣV) multiplied by the product of a pair of learning-rate parameters (α and β) that are associated with the two events and where $1 \geq \alpha > 0$ and $1 \geq \beta > 0$. During Pavlovian conditioning, each signalled outcome presentation will be less surprising than the last; this is captured by increases in ΣV , producing a decline in the term $(\lambda - \Sigma V)$, which results in increasingly small increments in ΔV , yielding a negatively accelerating learning curve. SOP shares this property, which is achieved differently through associative priming (Section 3.3). On the first trial the signal and outcome’s conjoint A1 activity will be good and this will increase excitatory strength between them. On the next trial the signal’s excitatory strength will prime the outcome. The associative priming will be weak on the second trial but it will allow some overlap of the signal’s A1 elements and the outcome’s A2 elements (Fig. 3). Outcome elements that are not primed will be free to enter their A1 states on the second trial and this will produce some excitation. The ratio of excitation to inhibition will decrease as ΔV increases on each trial and ΔV will reach asymptote (λ) and at this point changes in excitation and inhibition are equal on each trial. Thus the Rescorla and Wagner model and SOP account for competition for a fixed quota of associative strength in the same way and this principle extends to other key associative phenomena such as blocking [64,65], super conditioning [74] and relatively validity [63]. SOP may be seen as a more complete model than Rescorla and Wagner’s because it operates in real time [75,76] and anticipates latent inhibition and its context specificity [77], some perceptual learning phenomena [78], and modulation of UCS processing [76,79].

3.4. Decay priming and object recognition

The conclusions of this and the following section are summarised in Fig. 4.

It may already be obvious that the learning process described by SOP for Pavlovian conditioning (Sections 3.2 and 3.3) may apply to other stimuli, including those used in object recognition experiments with rodents. Although we might conceive of the representations of objects as being more complex than those of a pure

SOP Mechanism			
		Decay Priming?	Association Priming?
Type of object recognition	Spontaneous object recognition P P < Q	Yes.	Yes.
	Relative recency P Q P < Q	Yes.	No.
	Object in context xP & yQ xP < xQ	No.	Yes.

Fig. 4. Priming mechanisms in object recognition. The first column represents the experimental designs of the three forms of object recognition procedure (see Section 2.2). The pipe character (“|”) represents separate training stages. P and Q refer to distinctly different objects; x and y refer to distinctly different contexts. The SOP model of memory (e.g., Brandon et al.) specifies two qualitatively different activity states for stimulus representations: A primary state, A1, and a “primed” secondary state, A2. Stimulus elements may be primed into A2 states either by decay (i.e., sometime after recent stimulus presentation) or by associative activation (i.e., following the presentation of a second, associated stimulus). Both processes could occur in spontaneous object recognition: At shorter retention intervals object P’s elements are likely to be primed by decay from their recent A1 states, whereas at longer retention intervals priming is likely to be the result of the operation of a context \rightarrow object association. Decay and associative priming are, respectively, likely to be key mechanisms of relative recency and object-in-context.

tone, and composed of elements corresponding to multiple sensory domains, the same processes can be applied.

3.4.1. Spontaneous object recognition

The rodent's initial encounter with object P during spontaneous object recognition will generate A1 activity in the representational elements that provoke strong approach behaviour. After some time this behaviour will weaken, corresponding to the object-P elements' entry into their A2 state. Test presentation during this time would result in the standard bias towards exploration of the novel object, Q because its representational elements can pass freely from their inactive states to their A1 states whereas the elements of P that are still in the A2-state cannot.

3.4.2. Relative recency

We noted above (Section 2.2) that spontaneous object recognition performance worsens when a retention interval is interpolated between the pre-exposure and testing [50–52]. One of SOP's explanations of this is that longer retention intervals allow a greater proportion of P's elements to return from their A2 to their inactive states. Thus, on test, both P's and Q's inactive elements can pass directly to their A1 states where they can elicit similar, strong levels of approach. Demonstrations of relative recency [13,26–31] receive an identical explanation from SOP: The pre-exposure of P and then of Q will elicit A1 activity in their elements that will, over time, decay to A2 and then inactive states. Because P is pre-exposed before Q it is possible to arrange for testing with P and Q at a time when P's elements tend to be inactive but Q's elements remain in their A2 states. Here P's elements are free to enter their A1 states where they elicit strong approach; but many of Q's elements may remain in their A2 states and only weak approach is elicited.

3.4.3. Object-in-context

The most natural SOP account of object-in-context learning is described fully below (Section 3.5.1) and relies on the operation of associations between each context and the object that has been pre-exposed in it (i.e., $x \rightarrow P$ and $y \rightarrow Q$). Testing in context x will prime object P's elements but not object Q's. Thus the presence of P and Q on test in x will allow Q's elements to enter their A1 states from their inactive states, where they can elicit relatively strong approach; but P's primed elements will remain in their A2 state, unable to elicit such responding.

Although such associative-priming processes seem plausible, it is important also to consider possible decay-priming processes in object-in-context learning. The temporal asymmetries described for relative recency are also possible in object-in-context learning when a single trial of each type is used: Here there are two possible sequences for the object and context pre-exposures (i.e., either xP, yQ or yQ, xP). Of course, this is precisely the arrangement of object pre-exposure in a relative recency experiment, and so SOP anticipates that the first-pre-exposed object will provoke strongest approach, based on decay priming. The associative-priming mechanism predicts greater approach of Q than of P on test in context x, in which it is unexpected. Thus, decay- and associative-priming will oppose one another (i.e., weakening discrimination) but pull in the same direction (i.e., enhancing discrimination) with the yQ, xP pre-exposure sequence. We have recently found evidence of such interactions between associative and decay priming (Tam, Bonardi, & Robinson, report under review).

Although decay priming appears to influence performance in object-in-context learning, it cannot adequately account for it. There are two reasons for this statement: First, in experiments in which only a single xP and yQ trial is given [33–38], object-in-context learning is detected when performance over the two possible pre-exposure sequences is collapsed. That is, although differences in decay priming appear to operate, they will assist and

hinder discrimination performance in equal measure over both pre-exposure sequences. The fact that test discrimination is successful implies the operation of a second process over and above decay priming; second, it is possible to arrange multiple pre-exposure trials so that for each rat, on average, objects P and Q have been presented equally recently before testing. This is achieved by presenting xP and yQ pre-exposures multiple times, e.g., xP, yQ, yQ, xP for half of the subjects and yQ, xP, xP, yQ for the remainder and also results in object-in-context learning [32].

Thus, it appears that decay priming is required to explain relative recency but cannot accommodate object-in-context learning. Decay priming could also explain spontaneous object recognition.

3.5. Associative priming and object recognition

3.5.1. Spontaneous object recognition

Brandon et al. anticipate a second, association-based source of spontaneous object recognition: Context cues enter into excitatory associations with object P's representational elements during object P's pre-exposure (see, e.g., [18,21,43]). Thus, context cues will generate A2 activity (but not A1 activity) in object P's representational elements on testing. As with the decay-based source of performance, the associative source is based on the elements for object A tending to be in their A2 states, while those for object Q tend to be in their A1 state at the point of testing. Thus it seems that both associative and decay priming could support spontaneous object recognition.

3.5.2. Relative recency

In the case of relative recency, any such context \rightarrow P association will be matched by a context \rightarrow Q association and so test discrimination cannot obviously be accounted for by associative priming. However, non-reinforcement of a signal may extinguish excitatory learning [80,81] and follows SOP's rules (i.e., the non-reinforced signal will elicit A2 activity in the outcome's representation that will generate inhibitory associative learning). Thus any context \rightarrow P association could undergo extinction during the subsequent pairing of the context with Q, during which P is absent. Thus test performance could be based entirely on associative priming because, during testing, the context will be better associated with Q than with P. This will produce better priming of Q than of P, leading to the observed difference: greater approach of P than Q. However, studies show that multiple non-reinforced trials are necessary to achieve appreciable extinction [80,81] – unlike the single trial necessary for relative recency. Thus, although an associative priming account of relative recency is logically possible it is empirically improbable, and this indicates decay priming as the sole source of performance.

3.5.3. Object-in-context

The most direct evidence for the operation of context \rightarrow object associative priming comes from object-in-context tasks [32–38]. As we noted above (Section 3.4.3), accounts of object-in-context learning based on decay priming are implausible and so, by elimination, the associative priming account seems the most realistic component of the SOP model available to explain performance.

3.6. Conclusions about the roles of decay and associative priming in object recognition

We are left with the conclusion that associative priming is necessary to explain object-in-context learning, but that it cannot fully accommodate relative recency. This is the complementary arrangement to that of decay priming: Decay priming appears necessary to explain relative recency but is unlikely to account for object-in-context learning. Spontaneous object recognition is unusual in that it could operate by either form of priming. Perhaps, by modelling

parameters (timing, stimulus duration, etc.), we could manipulate the mix of decay and associative priming in spontaneous object recognition. But the unavoidable conclusion is that, according to SOP's analysis, spontaneous object recognition is an imprecise tool and is unsuitable for understanding separable psychological processes. The mixed findings on the effects of hippocampus lesions on rats' spontaneous object recognition (cf. [23,40,50] and [22,39]) may be explicable if it is assumed, say, that associative priming is dependent on the hippocampus and is more prominent in the procedures of those finding lesion effects than those who have not (cf. [18]). This logic applies to other manipulations, of course: For example, extension of the retention interval between pre-exposure and test will have a devastating effect on spontaneous object recognition that is largely dependent on decay priming, but one based largely on associative priming will be unaffected. But the discussion here implies that relative recency and object-in-context learning are relatively selective tools for examining decay and associative priming respectively.

Spontaneous object recognition has been described as a form of *habituation* (7), see also, [8,9] – that is, a decline in the behaviour that is elicited by a stimulus when it is presented repeatedly or over a long period of time. In the case of spontaneous object recognition the stimulus is object, P and the measured response is approach or exploratory behaviour. The decline in this behaviour may be assumed to occur during preexposure but is measured in the test relative to object Q. The stimulus specificity shown here meets a key feature of habituation. Several authors have noted that habituation can be understood as the result of a decline in the efficacy of the pathway between a stimulus and response [82]. It is quite possible that simple, stimulus-response based adaptive process may occur alongside those anticipated by SOP. One implication of this is that neural manipulations may affect SOP-based processes and spare stimulus-response based processes (e.g., [8,9,58]), or vice versa.

Sokolov ([83], see also [84,85]) described a model of habituation in which the presentation of a new stimulus will lead to the development of a representation of it. Prolonged or repeated presentation of the stimulus will foster increasing detail of that representation until it is entirely accurate. The process of representational modification is assumed to be the result of a mismatch in memory – that is the stimulus is compared with sets of stimulus representations in memory. When comparison finds a match, no representational modification is required; when comparison fails to find a match a new representation is assembled (or a close match is improved). In an habituation procedure, improvements in stimulus representation will be associated with declines in unconditioned response (i.e., habituation). Like Sokolov's model, the SOP model [15] allows for the assembly of stimulus representations – when their elements are concurrently in their A1 states – but no additional process of comparison takes place. Rather, changes in responsiveness to repeatedly presented stimuli are based solely on the priming principles outlined above.

4. Evidence of associative processes in object recognition

We have seen that SOP can be applied to standard demonstrations of object recognition. Of course, the mere fact that this model fits the data does not demand that the model should be accepted. We next describe some evidence from analytical object recognition experiments that make a stronger case for this position.

4.1. Enhanced spontaneous object recognition when multiple pre-exposures are spaced

We saw that spontaneous object recognition test performance could be the result of object P's representational elements

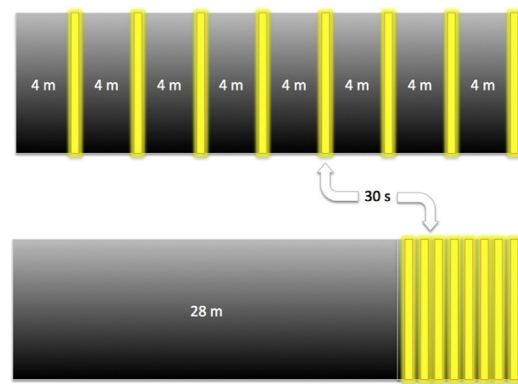


Fig. 5. Spaced and massed pre-exposure illumination. Schematic of Whitt and Robinson's [44] multi-trial pre-exposure in spontaneous object recognition. Rats were presented with object P during pre-exposure, which was only visible during eight 30-s periods of illuminations—contexts were otherwise darkened. The periods of darkness differed across two conditions, being either 4-min (spaced condition) or 30-s (massed condition). Subsequent discrimination (greater approach to object Q than object P) was superior in the spaced condition than in the massed condition.

becoming primed through a mix of decay and associative priming, which may vary according to the precise experimental parameters (e.g., the pre-exposure-test retention interval). To the extent that associative priming is involved in test performance, it will be important to maximise the strength of the context → object association during pre-exposure. As we saw above (Section 3.3), learning about the context → object relationship will occur only when the context's representational elements are in their A1 states, and the *valence* of this learning (i.e., whether it is excitatory or inhibitory) will depend on the activity state of the object's representational elements: When they are in their A1 states the association will be strengthened through additional excitation, but the association will be weakened by inhibition when they are in their A2 states.

Such weakening of the context → object association is expected when the object, P has been recently presented, as a result of decay-based priming. Several authors have reported that when multiple pre-exposures to object P are given, test performance is better when these pre-exposures are relatively well-spaced (e.g., [20,44,86]) and we have unpublished demonstrations of analogous effects in human participants' performance on an auditory recognition memory task. The pre-exposure schedule used by Whitt and Robinson is represented in Fig. 5. To ensure full experimental control over stimulus scheduling, objects P and Q were presented in glass cylinders, rendering them entirely visual stimuli. All rats received eight, 30-s periods of illumination during a single pre-exposure session, during which time they remained in the context. Object P would only have been visible during these periods of illumination. Rats' test performance following *spaced* pre-exposure, in which the interval between each illumination period was 4 min, was superior to that following *massed* pre-exposure, in which it was only 30 s. Our interpretation is that an appreciable proportion of the objects' representational elements returned to inactivity during the four-min inter-illumination period and were available to enter their A1 states on the subsequent period, thus supporting the formation of the context → object association. However, the massed pre-exposure trials occurred when P's elements were more likely to be primed. This will have produced some inhibitory x-P learning that would act to offset the excitatory x-P learning upon which performance partly relies.

4.2. Decay priming in relative recency

The decay-priming analysis of relative recency (Section 3.4.2) predicts that test performance will be highly dependent on the

	Preexposures & Intervals				Test	Interpretation
	P	Interval	Q	Interval	Result	Interpretation
Tam et al. (2014)	P	5 minutes	Q	5 minutes	P = Q	P and Q in A2
	P	2 hours	Q	5 minutes	P > Q	Inactive P able to enter A1. Q in A2.
Mitchell & Laiacona (1998)	P	1 hour	Q	Immediate	P > Q	Inactive P able to enter A1. Q in A2.
	P	1 hour	Q	24 hours	P > Q	?
	P	1 hour	Q	72 hours	P = Q	Inactive P and Q able to enter A1.

Fig. 6. Temporal manipulations in relative recency. Schematic of the temporal manipulations in pre-exposure-trial and retention-interval spacing in two relative-recency experiments. Rats in both experiments received sequential pre-exposure trials with objects P and Q before testing with the two objects. Tam et al. used a five-min retention interval between pre-exposure to object Q and testing. The duration of the interval between the two pre-exposure trials was either 5 min or 2 h; discrimination was better with the longer interval. Mitchell and Laiacona fixed the pre-exposure inter-trial interval (at 1 h) and manipulated the retention interval. Test discrimination was good at retention intervals of 24 h or less, but was absent at 72-h intervals. Note: Mitchell and Laiacona included additional intervals, which are not summarised here.

duration of the inter-trial intervals. For example, with a sufficiently short retention interval (i.e., the time between the final pre-exposure and testing), the interval between pre-exposure to P and Q becomes crucial in ensuring that P's elements are largely inactive by test. Tam, Robinson, Jennings, and Bonardi [87] have confirmed this prediction of SOP in a design that is summarised in Fig. 6. They presented rats with pairs of objects, P and Q, with a five-min interval between Q and the test. In one condition the interval between P and Q was also 5 min, and in another 2 h. The 2-h P-Q interval produced markedly stronger discrimination than the five-min P-Q interval. Tam et al. demonstrated that this time-related reduction in performance was not a general deficit, by showing a variant of object-in-context learning to remain unaffected by a similar manipulation of the interval between training and test. It is also notable that the analysis of object-in-context learning (Section 3.5.1) anticipates this insensitivity because the associative priming on which it relies will be unaffected by changes in the passage of time.

A related prediction is that relative recency should also be abolished by an extension of the retention interval (i.e., the interval between the second pre-exposure trial and test). When sufficiently long, the retention interval will allow the elements of both P and Q to become inactive so that, on test, A1 activity in both may be generated and similar levels of approach elicited. Mitchell and Laiacona [29] report just such a finding. Rats in three groups received pre-exposure to object P before object Q, which was separated by a 1-h interval. Test approach of Q was greater than P when testing occurred immediately after the pre-exposure to P, but with the interpolation of a 72-h retention interval test performance was attenuated. However, one feature of Mitchell and Laiacona's results is problematic for SOP: Relative recency discrimination was seen also in a group with a 24-h retention interval. In order to explain this pattern of results the analysis of relative recency outlined in Section 3.4.2 needs to assume that P's elements have decayed to inactivity at 25 h, but that at 24 h Q's remain largely primed in their A2 states. While this is not impossible, it could be seen as a surprising coincidence; given their potential theoretical significance, Mitchell and Laiacona's findings would benefit from confirmation and further analysis.

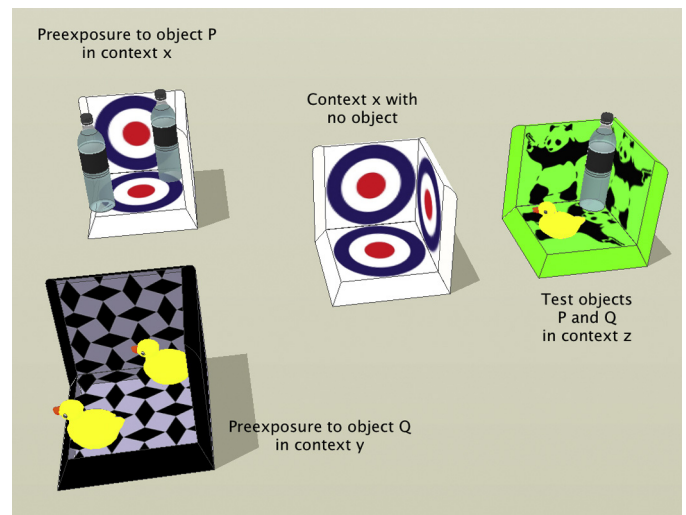


Fig. 7. Schematic of primed object-in-context. Schematic of an object-in-context experiment (e.g., Whitt, Haselgrove, & Robinson) in which the three stages of the experiment occur from left to right. The procedure began with rats receiving pre-exposure to object P in context x and with pre-exposure to object Q in context y, as in the standard object-in-context task. Next rats were placed in context x; no object was present but this treatment should be sufficient to allow the associative priming of object P. In the subsequent test, rats were presented with both objects, P and Q, but in a third context, z, which was associated with neither object. On test, rats approached Q in preference to P despite testing not occurring in P's context, x. Performance is consistent with the priming mechanisms.

4.3. Associative priming of object-in-context learning

The current analysis of object-in-context learning (Section 3.5.3; see Fig. 3) relies on the associative priming of object P by the test context, x. This priming of P usually occurs during the rodents' placement in context x at test. However, according to the analysis suggested here, this is not necessary: The only requirement is that x is primed at the time that x and y are tested. In order to examine this suggestion Whitt Haselgrove and Robinson [43] used the procedure summarised in Fig. 7. Exactly as in a standard object-in-context learning task, rats were initially presented with object P in context x and object Q in context y, to allow the establishment of $x \rightarrow P$ and $y \rightarrow Q$ associations. In a subsequent stage rats were placed in context x, but this contained no objects. This stage was intended to associatively activate object P's representation, and this priming was assumed to remain appreciable over the short time before testing. Unlike standard object-in-context learning, testing with objects P and Q occurred in a third context (e.g., z) in which no objects had been experienced. Despite this change in procedure, and consistent with SOP, rats approach was biased towards object Q relative to object P.

5. Discussion

We have attempted to apply the associative model of memory, SOP [16–18] to three representative forms of object recognition that are popular procedures in experimental psychology and behavioural neuroscience. In considering its dynamic processes (decay and associative priming) and its rules for association formation, SOP produced a satisfactory account of object memory. Experimental evidence [20,43,44,88] largely, though not universally (Section 4.2) supported SOP's account's of object recognition.

We touched briefly on alternative accounts of object recognition memory. For example, it has been suggested that object-in-context memory may reflect mnemonic processes like those in human episodic memory (e.g., [14]) and that relative recency may involve

a higher form of temporal memory (e.g., [13]). There is nothing in the preceding discussion to inform on the status of these intriguing and important possibilities but they are probably more complex explanations that are required to explain available findings. More troubling for such accounts is that the evidence described here supports direct predictions from SOP. It is possible of course that these findings could also be interpreted in terms of more sophisticated memory systems, though it is unclear to us how this could be done and it is probably unnecessary to do so. Being based on a large body of experimental evidence from the study of habituation and Pavlovian conditioning, SOP can be used to deliver several testable areas of experimentation that could further evaluate this account of recognition memory.

Disclosure statement

Neither author is aware of any conflict of interest created associated with this report.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.bbr.2014.10.046>.

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