Neurobiology of Learning and Memory 108 (2014) 96–103

Contents lists available at SciVerse ScienceDirect

Neurobiology of Learning and Memory

journal homepage: www.elsevier.com/locate/ynlme

Review

Associative structures in animal learning: Dissociating elemental and configural processes

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ARTICLE INFO

Article history:
Available online 13 June 2013

Keywords:
Elemental
Configural
Hippocampus

ABSTRACT

The central concern of associative learning theory is to provide an account of behavioral adaptation that is parsimonious in addressing three key questions: (1) under what conditions does learning occur, (2) what are the associative structures involved, and (3) how do these affect behavior? The principle focus here is on the second question, concerning associative structures, but we will have cause to touch on the others in passing. This question is one that has exercised theorists since Pavlov's descriptions of the conditioning process, where he identifies the shared significance of the study of conditioned reflexes for psychologists and neuroscientists alike.

1. Historical orientation

> "*Hence, the temporary nervous connexion is a universal physiological phenomenon both in the animal world and our own. And at the same time it is a psychic phenomenon, which psychologists call an association, no matter whether it is a combination of various actions or impressions, or that of letters, words, and thoughts. What reason might there be for drawing any distinction between what is known to a physiologist as a temporary connexion and to a psychologist as an association? Here we have a perfect coalescence, a complete absorption of one by the other, a complete identification. Psychologists seem to have likewise acknowledged this, for they (or at any rate some of them) have made statements that experiments with conditioned reflexes have provided associative psychology……with a firm basis.*"

Pavlov (1935; The Conditioned Reflex; taken from: Lectures on Conditioned Reflexes (Volume 2): Conditioned Reflexes and Psychiatry, p. 167, 1941).

For Pavlov then, conditioned reflexes were a means of measuring, noninvasively but remotely, the formation of associative links in the brain; a sentiment echoed by Konorski (1967) who stated that "*the conditioned response [is] playing the role of a 'tracer' allowing the association to be detected.*" However, these authors also raised the prospect of a rapprochement between an associative analysis of learning, on the one hand, and its neural instantiation, on the other hand. The field of animal learning theory, while largely eschewing this prospect, has aimed to answer three fundamental questions about the nature of the conceptual nervous system through the lens provided by conditioned behavior: under what conditions does learning occur, what is the nature of the associative structures that underlie learnt changes in behavior, and how is learning translated into performance? However, as we hope to show, the analytic tools developed in the service of this aim, together with the resulting insights that their use provides, can shape our understanding of the brain mechanisms that underpin learning and memory; and the reverse is also true: neuroscientific analysis can permit a resolutions to theoretical issues that have proven, if not intractable, then certainly elusive.

2. Associative structures: conditioning and sensory preconditioning

For an extended period, during the first part of the 20th century, learning theory provided a theoretical framework that was both parsimonious and dominant. The essential idea was that learning in animals could be explained by the formation of associative links between the processes that are concurrently activated by a stimulus (S) and a response motor program (R) when both are followed by a reinforcer (e.g., Hull, 1943; Thorndike, 1911). This idea is certainly parsimonious: even in bare outline, it provides simple answers to all three of the questions posed above: The *conditions* required for learning are that the processes activated by the critical events (the S and R) occur close together in time and are "stamped in" by contingent reinforcement; the *content* of learning takes the form of an S → R link; and learnt behavior is manifest in *performance* to the extent that the presentation of the stimulus is able

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1074-7427/$ - see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.nlm.2013.06.002

to activate the response motor program via the link that has formed between their corresponding processes. Such prosaic theorizing is admirable, but in each case the answers provided by S → R theory turned out to be incomplete.

Take the example of sensory preconditioning (SPC), which will have continuing relevance throughout this article: After two neutral stimuli have been paired (e.g., a light with a tone; e.g., Brogden, 1939) directly establishing a conditioned response to the tone (by pairing it with shock) also results in the light eliciting responding. In this case, light-tone pairings result in learning without obvious reinforcement and which is behaviorally silent (for further discussion, see Honey, Good, & Manser, 1998a; Honey, Watt, & Good, 1998b). Demonstrations of SPC undermine a simple S → R analysis of the nature of associations that underpin animal behavior (p. 85–87, Mackintosh, 1974), and suggest a need to consider alternative associative structures.

Two candidate associative structures have often been advanced in the context of discussions of SPC, and standard forms of conditioning alike: elemental and configural. As we shall see, both of these types of structure can underpin the process of pattern completion: re-creation of a training episode from the presentation of one of its components; and pattern separation: enabling training episodes with overlapping components to be represented as separate memories. The elemental analysis holds that the central processes or memories activated by events (e.g., the light and tone) become directly linked to one another by an *elemental* association (see left side of Fig. 1). In contrast, the configural analysis holds that these processes become linked to some third, independent *configural* representation that then codes for their co-occurrence (see right side of Fig. 1). The elemental and configural accounts provide a ready account for simple demonstrations of SPC. For example, the two elementary associations resulting from the light → tone and tone → shock pairings can form an associative chain that allows the light to provoke a memory of shock and thereby a conditioned response at test (but see also, Lin & Honey, 2011; Lin, Dumigan, Dywer, Good & Honey, 2013; Ward-Robinson & Hall, 1996). According to a configural analysis, the light and tone become linked to a separate configural unit, which is later (i) linked to shock during tone → shock pairings, and (ii) mediates responding to the light at test. This configural analysis might appear to be contrived, especially when applied to what is learnt during the simple pairing of two stimuli. However, there is evidence from both studies of conditioning and parallel studies of SPC showing that a configural analysis should not be dismissed (e.g., Iordanova, Good, & Honey, 2008). In fact, there is now compelling neuroscientific evidence, that we shall come to later, suggesting that both elemental and configural associative structures are acquired during exposure to patterns of stimulation. But, for now, we need to consider briefly evidence showing that animals can acquire configural associations, and how this evidence has been addressed by theories of associative learning.

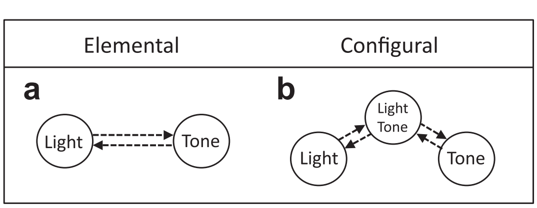

Fig. 1. (a) Elemental and (b) configural associative structures that could provide the basis for demonstrations that rats learn that two stimuli co-occur (e.g., during SPC procedures).

3. Standard configural discriminations

One impetus for the idea that animal behavior can be based on the formation of configural associations is straightforward: They can solve discriminations that should prove impossible if they were reliant on *purely* elementary associations. For example, in a configural discrimination, rats might be placed in two visual contexts (A and B; e.g., chambers with spotted or checked wallpapers) and receive separate presentations of two auditory stimuli (X and Y; e.g., a tone and clicker). In context A, presentations of X are paired with food while those of Y are not, and in B presentations of Y are paired with food and those of X are not. The fact that both of the contexts, like both of the auditory stimuli, are equally often paired with food (and no food), means that animals only capable of forming elemental associations might come to show conditioned responding (approaching the site of food delivery) when placed in either context and presented with both auditory stimuli; but they should not show more conditioned responding during the reinforced configurations (AX and BY) than during the nonreinforced configurations (AY and BX). The fact that they do means that a *purely* elemental analysis is unsustainable. However, more complex elemental analyses have been developed that are capable of explaining how configural discriminations are learnt. According to these analyses, the memorial elements that are activated by a compound stimulus (AX) are not a simple product of those that are activated by separate presentations of A and X. For example, it has been proposed that each of the four context-auditory stimulus combinations (i.e., AX, BX, AY, and BY) gives rise unique elements (i.e., ax, ay, bx, and by; Wagner & Rescorla, 1972); or that each stimulus (e.g., X) might activate a set of elements (cf. Atkinson & Estes, 1963) the composition of which is affected by whether it is presented in one context (A) or another context (e.g., B; Wagner, 2003). Even without further elaboration, but noting the combinatorial explosion with increases in the number of stimuli in a compound, it is clear that these modifications allow an elemental analysis to be developed for the acquisition of configural discriminations: The elements that are uniquely activated by a given combination of stimuli become linked to the outcome of the trial, and thereby provide a basis for conditioned responding to be more evident during the reinforced compounds (AX and BY) than the nonreinforced compounds (AY and BX).

There is evidence (for a review, see Honey, Close & Lin, 2011) that is already troublesome for both modified elemental theory (e.g., Wagner, 2003) and purely configural theories (e.g., Pearce, 1994). Leaving aside this evidence, however, there is one straightforward prediction that unites both analyses: It should not be possible to observe a clear-cut dissociation between discrimination learning problems according to whether they are (operationally) elemental or configural. This prediction follows from the assumptions that all discriminations involve a single system that instantiates the same type of associative structure: either elemental or configural. It is just such a dissociation that has been recently observed using variants of a SPC procedure.

4. Dissociating elemental and configural structures in sensory preconditioning

We have recently developed a novel set of behavioral assays that can be defined operationally as elemental or configural. Both types of assay involved rats encountering different auditory stimuli (X and Y) in different contexts (A or B) and at different times of day (morning and afternoon). The choice of these stimuli was motivated, at least in part, by claims that animals can form memories that integrate the components of episodic memory: what happened (X or Y), where (context A or B) and when (morning or