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Conjunctive representations, the hippocampus, and contextual fear conditioning

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The context in which events occur can be represented as both (1) a set of independent features, the feature representation view, and (2) a set of features bound into a unitary representation, the conjunction representation view. It is assumed that extrahippocampal (e.g., neocortical) areas provide a basis for feature representations, but the hippocampal formation makes an essential contribution to the automatic storage of conjunctive representations. We develop this dual-representation view and explore its implications for hippocampal contributions to contextual fear conditioning processes. To this end, we discuss how our framework can resolve some of the conflicts in the recent literature relating the hippocampus to contextual fear conditioning. We also present new data supporting the role of a key mechanism afforded by conjunctive representations—pattern completion (the ability of a subset of a memory pattern to activate the complete memory)—in contextual fear conditioning. As is implied by this mechanism, we report that fear can be conditioned to the memory representation of a context that is not actually present at the time of shock. Moreover, this result is predicted by our computational model of cortical and hippocampal function. We suggest that pattern completion demonstrated in animals and by our model provides a mechanistic bridge to human declarative memory.

The events of our lives take place against a background of cues that provide a place, space, or context for experience. Moreover, the stimulus features that make up this background play a major role in retrieving specific memories. Thus, knowing exactly how the brain represents background or context has important implications for memory processing in general. On psychological grounds, one can identify two orthogonal ways in which the elements of a context can be represented: the *features view*, where context is represented as a set of independent features or elements that each can enter into association with an event, and the *conjunctive view*, where the separate features are bound into a new unitary representation that encodes their conjunction or cooccurrence.

These *dual representations* of context have been mapped onto distinct neurobiological substrates. Nadel and Willner (1980; Nadel, Willner, & Kurz, 1985) have suggested that neocortical systems are able to represent the independent features of the environment and provide a basis for feature-to-feature association, whereas the elaboration of features into a unitary representation of a place or a location requires that the cortex interacts with the hippocampus. Following O'Keefe and Nadel (1978), Nadel and his colleagues call this hippocampal-dependent representation a *cognitive map*. More recently, other researchers have referred to the elaborated representation as a *unitary representation* (e.g., Fanselow, DeCola, & Young, 1993), a *configural association* (Sutherland & Rudy, 1989), or a *conjunctive representation* (O'Reilly & Rudy, in press; Rudy & O'Reilly, 1999).

The goal of this paper is to elaborate the dual-representation view of how the brain represents context and to explore the implications of these ideas for understanding contextual fear conditioning. We begin with an introduction to contextual fear conditioning and establish the idea that it depends in part on conjunctive representations of context that are supported by the hippocampus. Next, we constrain the idea that the hippocampus encodes conjunctive representations and discuss the advantages that conjunctive representations have over feature representations. We then establish, in more detail, the relationship between the hippocampus and contextual fear conditioning. The dual-representation view of context conjunctive representation is then discussed in relationship to the apparently differential effects produced by damaging the hippocampus prior to (*anterograde* effects) versus after (*retrograde* effects) contextual fear conditioning. The behavioral implications of the conjunctive view for understanding why context preexposure can facilitate contextual fear conditioning are then presented, along with new experiments that support the conjunctive view. Finally, our computational model is described and applied to the new data that we present.

Contextual Fear Conditioning

The contextual fear conditioning paradigm provides a useful venue for exploring the dual representations of context. In a typical fear conditioning experiment, a rat is placed into an apparatus and receives pairings of a phasic auditory cue and electrical shock to its feet. Subsequently,

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when the auditory-cue conditioned stimulus is presented, the rodent will display a natural defensive response termed *freezing*—it becomes immobile. In addition to displaying conditioned freezing to the auditory cue, however, the rat also displays freezing to the situation or place in which the shock occurred. This phenomenon is usually referred to as *contextual fear conditioning*, and it is the primary focus of this paper.

By itself, the observation that the rat displays fear to the place where shock occurs does not distinguish between a features-based and a conjunctive-based representation view. In fact, given that the rat conditions strongly to a single phasic auditory cue, one would think that conditioning to one or more of the several independent features that make up a context (e.g., its smell, illumination, floor texture, or chamber geometry) would be more than sufficient to support the fear response. In addition, there are no extrinsic demands on the subject to construct a conjunctive representation of the cooccurring features that make up the context.

Nevertheless, there are good reasons to believe that a features representation view alone cannot provide an adequate account of contextual fear conditioning. Two phenomena in particular suggest that contextual fear conditioning requires a dual-representation account. First, there is evidence that contextual fear conditioning, but not auditory-cue fear conditioning, is compromised by damage to the hippocampus (Kim & Fanselow, 1992; Phillips & LeDoux, 1992). This finding is consistent with the early suggestions that the hippocampus supports conjunctive representations (Nadel & Willner, 1980; Nadel et al., 1985).

An additional link between contextual fear conditioning and conjunctive representations emerged from Fanselow's (1990) analysis of the so-called *immediate-shock effect* (Blanchard, Fukunaga, & Blanchard, 1976). The rat will display fear to the context if placed in the conditioning chamber for about 1 min before the shock. However, if it is shocked *immediately* after being placed in the chamber, the rat will show almost no freezing. The important observation Fanselow (1990) made was that exposing the rat to the context prior to the shock session significantly attenuated the immediate-shock effect—preexposed rats subsequently displayed conditioned freezing (see also Kiernan & Westbrook, 1993; Westbrook, Good, & Kiernan, 1994).

Fanselow (1986, 1990) argued that context fear depends on the rat's acquiring a conjunctive representation of its features (he used Pavlov's term *dynamic stereotype*, but the meaning is the same). Rats shocked immediately after being placed into the context did not have the opportunity to acquire this representation. Preexposure to the context provides an opportunity for the rat to construct the conjunctive representation. Thus, provided that this representation is activated at the time of shock, contextual conditioning will be acquired.

Together, these findings encourage two key ideas: (1) Contextual fear conditioning depends on a conjunctive representation of contextual features, and (2) this conjunctive representation is encoded in the hippocampus. Similar ideas about contextual fear conditioning have been offered by a number of researchers (Fanselow, 1999, 2000; Fanselow & Rudy, 1998; Maren, Aharonov, & Fanselow, 1997; O'Reilly & Rudy, in press; Rudy & O'Reilly, 1999; Rudy & Sutherland, 1992, 1994, 1995).

Conjunctive Representations and the Hippocampus: Some Constraints

Variations on the idea that the hippocampus contributes to memory by binding together the features of a situation to create a unitary/conjunctive representation of an experience have been central to many accounts of the role of the hippocampus in memory (Marr, 1971; McNaughton & Nadel, 1990; O'Keefe & Nadel, 1978; Squire, 1992; Sutherland & Rudy, 1989; Tyler & DiScenna, 1986; Wickelgren, 1979). However, we have argued that, left unconstrained, this idea cannot be correct (O'Reilly & Rudy, in press), because there is clear evidence that rats with damage to the hippocampus can solve discrimination problems that require conjunctive representations of the controlling cues (see Rudy & Sutherland, 1995, for a review). This evidence was generated in response to Sutherland and Rudy's (1989) configural association account of hippocampal function. In their account, the hippocampus constructs configural (conjunctive) representations of compound stimuli that can then be used to control performance.

The configural association account made the strong prediction that rats with damage to the hippocampus could not solve nonlinear discrimination problems that require the construction of configural (conjunctive) representations. For example, consider a biconditional discrimination of the form AB+, CD+, AC−, BD−. In this problem, rats are reinforced (+) for responding in the presence of the AB and CD compounds but are not rewarded (−) for responding in the presence of the AC and BD compounds. The critical feature of this problem is that each element (A, B, C, D) is equally associated with rewarded and nonrewarded trial outcomes, so that the linear combination of the associative strengths of each element would be equal across the compounds. This combination rule cannot support differential responding to the reinforced (AB+ and CD+) versus nonreinforced (AC− and AD−) compounds of the biconditional problem. The only way this problem can be solved is for the rat to construct a conjunctive representation of the compounds and associate these unique representations with their respective trial outcomes. These are difficult problems and require many trials for animals to solve. Nevertheless, *both* intact rats and rats with virtually complete damage to the hippocampus can solve these problems (e.g., Alvarado & Rudy, 1995; Davidson, McKernan, & Jarrard, 1993; Gallagher & Holland, 1992; Whisaw & Tomie, 1991). Thus, the general idea that the hippocampus uniquely supports conjunctive representations cannot be correct (see O'Reilly & Rudy, in press; Rudy & Sutherland, 1995).

It is important to note that the reinforcement contingencies associated with nonlinear discrimination problems demand a solution that depends on the subject's constructing a conjunctive representation of the compound stimuli. In contrast, however, one can imagine that conjunctive representations might be established *automatically* just as a consequence of exploring and attending to the environment. Indeed, this assumption is embedded in the hypothesis that preexposure attenuates the immediate-shock effect by providing the rat the opportunity to acquire a conjunctive representation of context. This is because there are no explicit reinforcement contingencies present during preexposure that require the rat to acquire a conjunctive representation. If such a representation is acquired, it must be an automatic product of the rat's exploring the situation.

On the basis of the facts and arguments represented in the above paragraphs, we have concluded that it is important to recognize and discriminate between *two types of conjunctive learning* (O'Reilly & Rudy, in press; Rudy & O'Reilly, 1999): (1) conjunctive learning that requires considerable training and is forced by the contingencies of reinforcement that define a problem (e.g., nonlinear discrimination problems) and (2) conjunctive learning that occurs automatically and rapidly just as a consequence of the organism's actively exploring its environment. We further assume that it is the rapid and automatic form of conjunctive learning that is especially dependent on the hippocampus and that conjunctions learned gradually and forced by the contingencies of reinforcement can be supported by the neocortex.

We have embedded these ideas into an explicit computational neural network model that is able to integrate a wide range of findings relating hippocampal damage to learning and memory, including the nonlinear discrimination literature, habituation, incidental contextual learning, transitivity, and some phenomena associated with contextual fear conditioning (O'Reilly & Rudy, in press). We will explore in more detail the implications of some of these general ideas for contextual fear conditioning. However, it will be useful first to briefly discuss the power of a conjunctive representation relative to a features representation.

The Power of Conjunctive Representations

The first property of conjunctive representations that should be mentioned is that they will support what is sometimes termed *pattern completion* (Marr, 1971; McNaughton & Morris, 1987; O'Reilly & McClelland, 1994). When an input pattern of features (A, B, C, D, E) is conjoined into a memory representation, the presentation of a subset of the features (e.g., A, E) will activate the memory for the entire input pattern. Clearly, this ability of a subset to reactivate the whole is important for cued recall of stored memories, and it has been assumed to underlie hippocampus-dependent declarative memory in humans. For example, in his review of this literature, Squire (1992) suggested that "In the present account the possibility of later retrieval is provided by the hippocampal system because it has bound together the relevant cortical sites. A partial cue that is later processed through the hippocampus is able to reactivate all of the sites and thereby accomplish retrieval of the whole memory" (p. 224). One attractive reason to explore the implications of the conjunctive representation view of contextual fear is that it provides a way to link, at a mechanistic level, the animal literature with human declarative memory.

When two events are similar—composed of overlapping features (e.g., ABCDE and ABCEF)—the potential for interference is high. If these similar patterns are represented as unique conjunctions, however, interference can be reduced. Thus, a second property of conjunctive representations is that they produce *pattern-separated* representations of similar experiences or input patterns.

O'Reilly and McClelland (1994) provided a detailed argument for why the architecture of the hippocampus supports both pattern completion (see also McNaughton & Morris, 1987) and pattern separation. There are obvious tradeoffs between the demands of pattern completion and pattern separation. In pattern separation, similar inputs are encoded using distinct representations, whereas pattern completion requires that similar inputs (e.g., the original item and its subsequent retrieval cue) collapse onto the same representations. These tradeoffs have been discussed in detail by O'Reilly and McClelland (1994; see also O'Reilly & Rudy, in press).

Conjunctions in Contextual Fear Conditioning

The principle of pattern completion is at the heart of the conjunctive representation and explains (1) why a conjunctive representation will support more conditioning than its unconjoined features and (2) why context preexposure produces more conditioning in the immediate-shock paradigm. We will explore these effects in greater detail in the following sections but provide a brief overview here. In the first case, if the rat conditioned just to representations of features, the magnitude of the conditioned response would be a function of the amount of conditioning that had been acquired by the individual features the rat sampled during testing. However, if conditioning was based on a conjunctive representation of all the features, this representation could be activated by some subset of the features, and the level of fear expressed would be a function of the amount of conditioning to the entire set of features active in memory and would not be determined just by the individual features that happened to be sampled during testing. In the second case, pattern completion is the likely basis of the context preexposure advantage, because if the rat has acquired a conjunctive representation during preexposure, then when it is exposed to the context briefly, immediately prior to shock, the subset of features it sampled should activate the memory ensemble representing the context. Conditioning then will be to the entire set of features, as opposed to just the small subset of features that may or may not be sampled during testing. Consequently, even though the rat might sample only a subset of features during conditioning, during testing responding will be controlled by the entire memory ensemble, not just by the sampled features.

Hippocampal Conjunctive Representations Support Contextual Fear Conditioning

An obvious implication of the idea that hippocampal conjunctive representations support contextual fear conditioning effects through pattern completion is that damage to the hippocampus should reduce the magnitude of contextual fear conditioning. There is support for this prediction; however, the literature is not straightforward (Anagnostaras, Maren, & Fanselow, 1999; Frankland, Cestari, Filipkowski, McDonald, & Silva, 1998; Gewirtz, McNish, & Davis, 2000; Kim & Fanselow, 1992; Kim, Rison, & Fanselow, 1993; Logue, Paylor, & Wehner, 1997; Maren et al., 1997; Phillips & LeDoux, 1992, 1994; Richmond et al., 1999; Selden, Everitt, Jarrard, & Robbins, 1991). So a number of factors must be considered to bring some order to it, including (1) time of lesion, whether the hippocampus is damaged before (anterograde damage) or after (retrograde damage) training, (2) the lesion method (electrolytic or excitotoxic), and (3) the site of the lesion (dorsal, ventral, or complete lesion). We will briefly review the relevant data and then suggest an overall account that preserves the essential role of the hippocampus in conjunctive representations of context in fear conditioning, while also allowing for a possible role for features representations subserved by extrahippocampal areas.

Damage to the hippocampus after training (retrograde) consistently impairs contextual fear conditioning, whether the damage is induced by electrolytic or excitotoxic methods (Anagnostaras et al., 1999; Frankland et al., 1998; Kim & Fanselow, 1992; Maren et al., 1997). Damage to the hippocampus prior to training (anterograde) has produced varied results. Some researchers have reported positive results (Phillips & LeDoux, 1992, 1994), but there are also reports that prior damage to the hippocampus has no effect on contextual fear conditioning (Maren et al., 1997; Richmond et al., 1999). Furthermore, the effect of damaging the hippocampus prior to training appears to depend on both the lesion technique and the site of the lesion. Contextual fear conditioning is impaired by electrolytic damage to the dorsal hippocampus (Maren et al., 1997; Maren & Fanselow, 1998) and by excitotoxic damage to the ventral hippocampus or by excitotoxic damage to both the dorsal and the ventral hippocampus (Richmond et al., 1999). Excitotoxic damage to just the dorsal hippocampus, however, does not impair contextual fear conditioning (Maren et al., 1997; Richmond et al., 1999).

There is some agreement (see Fanselow, 2000; Maren et al., 1997; Richmond et al., 1999) that the anterograde impairment produced by electrolytic dorsal lesions and excitotoxic ventral and complete hippocampus lesions is due to hyperactivity that occurs because of damage to the ventral hippocampus directly (as in the Richmond et al., 1999, work) or because electrolytic damage to the dorsal hippocampus disrupts fibers projecting to the nucleus accumbens. Hyperactivity could, then, either interfere directly with the expression of the freezing response during testing or result in an abnormal sensory experience either during training or during testing. In either case, the impairment would be attributed to a performance deficit (see also Gewirtz et al., 2000). Although the ventral hippocampus may contribute to memories supported by the hippocampus, this contribution at present cannot be distinguished from performance effects that are associated with damage to it. Therefore, we are not inclined to consider the ventral hippocampus as supporting the conjunctive representation of context, even though it might.

There is sufficient evidence, however, to support the view that the *dorsal hippocampus* contributes to the learning and memory process supporting contextual fear conditioning. First, as was noted, damage to the dorsal hippocampus after training consistently impairs the retention of contextual fear conditioning independent of type of lesion. Moreover, Anagnostaras et al. (1999), using a within-subjects design, found that damage to the dorsal hippocampus disrupted contextual fear conditioning when given 1 day following training, but not when training occurred 50 days prior to lesioning. That the same rats expressed fear to the context when training was 50 days before the lesion but did not when training was 1 day before the lesion virtually rules out a performance interpretation of the role of the dorsal hippocampus. In addition, Bellgowan and Helmstetter (1995) reported that transiently disrupting dorsal hippocampus functioning by injecting musimol bilaterally into the dorsal hippocampus selectively impaired contextual but not auditory-cue fear conditioning. Similar results have been reported by Baily, Sun, Kim, and Helmstetter (1997) to occur when a protein synthesis inhibitor was injected into the dorsal hippocampus immediately following fear conditioning. Because, in both cases, the rats were tested in the normal state, it is difficult to attribute these findings to a performance impairment.

The data above strongly imply that the dorsal hippocampus contributes to the conjunctive memory processes that support contextual fear conditioning. Why, then, does damage to the dorsal hippocampus prior to training often not impair contextual fear conditioning? Clearly, extrahippocampal systems can support contextual fear. We noted at the outset that one can identify two positions about how the elements of a context can be represented: the features view—that the context is represented as a set of independent features or elements that each can enter into association with a phasic event (such as shock)—and the conjunction view. We also noted that these views are not mutually exclusive and that both representations can contribute to contextual fear conditioning. It is our view that the preserved contextual fear observed when the hippocampus is damaged prior to training depends on features-based association in extrahippocampal areas.

This dual-representation view also has been embraced by Maren et al. (1997; see also Fanselow, 2000) to account for the variability in anterograde effects. They suggested that two representations exist, but in a hierarchical relationship. The intact rat is biased to use the conjunctive representation over the features representation. Thus, when conditioned prior to the lesion, shock is associated with the hippocampal-dependent conjunctive representation at the expense of conditioning to the extrahippocampal features representation. So, when the dorsal hippocampus is removed after conditioning, there is a severe (retrograde) impairment. In contrast, removal of the hippocampus prior to conditioning frees up the extrahippocampal features system to support conditioning. So, given the right training parameters, one may not detect impaired fear conditioning, because the extrahippocampal system will compensate.

One could speculate, given a rapid-learning hippocampal conjunctive system versus a more gradual learning cortical-based features system, that factors such as the number of shock presentations could play a role in determining the contribution of the features representation system. It is generally the case that multiple shocks are given during training (e.g., Maren et al., 1997; Richmond et al., 1999). However, studies that systematically varied such parameters as shock number, shock intensity, and duration of time in the context before shock in combination with dorsal hippocampal damage would help greatly to clarify this situation.

To summarize, there is sufficient support for the idea that the hippocampus contributes to contextual fear conditioning, and further tests of the specific parameters for achieving preserved learning with anterograde lesions should be quite informative regarding the hypothesized differences in hippocampal versus cortical learning properties. Although we hypothesize that the hippocampus contributes via pattern completion of conjunctive representations, it is difficult to isolate this specific contribution, because both a features and a conjunctive encoding of context can contribute to the basic contextual fear response. Therefore, in the next section, we turn to the effects of context preexposure, to more clearly delineate the unique hippocampal contribution.

Context Preexposure Depends on Conjunctive Representations

We noted that preexposure to the conditioning context can significantly enhance the level of contextual fear normally produced by immediate shock. In addition, context preexposure has been reported to facilitate contextual fear conditioning under a variety of circumstances in which rats normally acquire very little fear. For example, Rudy and his colleagues have produced abnormally low fear conditioning (1) when rats were isolated immediately after conditioning (Pugh et al., 1999; Rudy, 1996), (2) if they were conditioned at noon instead of in the morning or late afternoon (Rudy & Pugh, 1998), (3) if they received posttraining injections of morphine (Rudy, Kuwagama, & Pugh, 1999), (4) if they were adrenalectomized prior to training (Pugh, Tremblay, Fleshner, & Rudy, 1997), (5) if they experience postconditioning treatments that stimulate the release of cytokine interlukin-1 beta (Pugh et al., 1998), or (6) if juvenile rats are tested 10 min after conditioning (Rudy & Morledge, 1994). In each of these cases, preexposure to the context restored contextual fear conditioning to control levels. Thus, there is little doubt that rats learn something about the context simply as a consequence of exposure and, presumably, exploration. The critical questions, however, are what do they learn and how does this facilitate the acquisition of contextual fear conditioning.

We have already noted how a conjunctive representation view can explain why context preexposure facilitates contextual fear conditioning. However, with suitable assumptions, a features-based view also can account for these effects. Specifically, preexposure could strengthen the representations of the individual features that collectively make up the context (we have termed this the *enhanced saliency* view; Rudy & O'Reilly, 1999). This enhanced saliency allows each feature to more easily associate with shock and thus facilitates the acquisition of contextual fear. To experimentally evaluate these two accounts, we focused on the principle of pattern completion, which is at the heart of the conjunctive account. There are at least four implications of this principle that can be evaluated to determine the validity of the conjunctive representation account: (1) The facilitating effect of context preexposure depends on a conjunctive representation; (2) pattern completion can enhance generalized fear; (3) pattern completion can support conditioning to a memory representation of a context; and (4) hippocampal lesions should impair preexposure effects.

The facilitating effect of context preexposure depends on a conjunctive representation. To appreciate the first implication, consider the following reasoning based on the conjunctive account. (1) Preexposure to the context enhances contextual fear conditioning because it provides the opportunity for the subject to store a conjunctive representation. (2) A conjunctive representation can only be acquired if the entire set of features that make up the context cooccur and are experienced. (3) Therefore, for preexposure to the context to facilitate contextual fear conditioning, *it is necessary that the subject experience the features of the context together.* Preexposure to just the individual features that make up the context should not facilitate contextual fear conditioning. In contrast, the enhanced saliency view asserts the following. (1) Preexposure enhances contextual fear conditioning because it increases the saliency of the individual features, thereby increasing the rate of conditioning to each feature. (2) Therefore, all that matters is that the subject experience all the features that make up a conditioning environment. *The features do not have to be sampled together.*

We have recently reported a strong test of these two views (Rudy & O'Reilly, 1999). In one experiment, we compared the performance of three groups of rats given different preexposure experiences. The rats in the *context* preexposure group were exposed to the conditioning context (Context A). The rats in the *feature* exposure group were exposed to the independent features of the conditioning context, but these features were not experienced together (Contexts B, C, and D). The rats in the *control* group were preexposed for a comparable period of time to a context that shared no features with the conditioning context, an opaque mouse cage. The exact details of this experiment can be found in Rudy and O'Reilly (1999). The top of Figure 1 illustrates the general methodology we used to construct the preexposure procedures that were used.

On the day of conditioning, each rat was placed into the conditioning chamber (Context A) and, 120 sec later, received an electrical shock to its feet. The rat was returned to the home cage for 10 min and then brought to the conditioning room, where it was tested for 5 min. We note that Rudy and Morledge (1994) reported that rats tested 10 min after conditioning displayed a markedly reduced level of freezing, as compared with their level of freezing 24 h after conditioning. They also reported that rats preexposed to the context 24 h before conditioning greatly increased the amount of freezing the rats displayed when tested with a 10-min retention interval. So, we used this procedure to assess the facilitating effect of context preexposure.

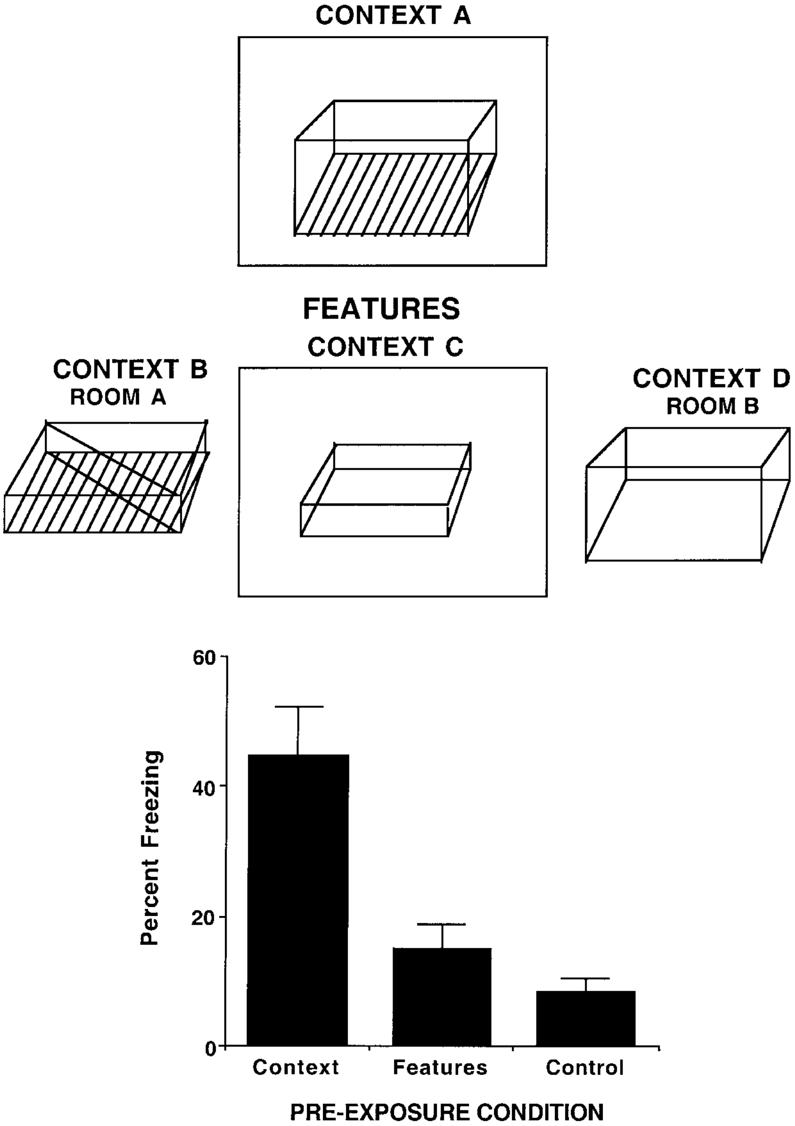

Figure 1. The top of this figure illustrates the methodology used to expose rats to the context (Context A) or to the unconjoined features that made up Context A (Contexts B and C). The rats in the context preexposure condition were preexposed to Context A, whereas the rats in the features preexposure condition were exposed to Contexts B, C, and D. The rats in the control condition were exposed to a different context (a mouse cage) not represented in this figure. The bottom of this figure presents the mean percentage of freezing as a function of the preexposure conditions just described. Bars represent standard errors of the mean.

The conjunctive account predicts that only rats preexposed to the conditioning context features together will benefit from preexposure, whereas the features account predicts that exposure to either the context or its component features will facilitate contextual fear. The results of this experiment (Figure 1, bottom) clearly supported the conjunction representation view of context. Note first that, consistent with Rudy and Morledge's (1994) finding, the rats in the control condition that had not been exposed to any of the features of the conditioning context displayed almost no freezing. Moreover, the rats in the features condition did not differ from the rats in the control condition. So, preexposure to the separate features of the conditioning context did not facilitate contextual conditioning. In contrast, preexposure to context itself greatly facilitated contextual fear conditioning. This pattern of results clearly favors the conjunctive representation view.

We also tested the conjunction versus enhanced saliency views, using a different preexposure treatment (Rudy & O'Reilly, 1999). The methodology for this experiment is shown in the top of Figure 2. It displays four contexts (A, B, C, D). Context C was the conditioning context, and Context D was composed of a different set of features. Contexts A and B together contained all of the same features as Contexts C and D together, but in different combinations. So, one set of rats (*context same*) was preexposed to Contexts C and D. They were subsequently conditioned and tested in Context C. Another set of rats was preexposed to Contexts A and B (*context shift*) but were conditioned in Context C. Rats in the *control* condition were exposed to an opaque mouse cage that contained none of the features of the conditioning context.

Because rats in the context same and context shift conditions had equal experience with the various features that composed the conditioning context, the enhanced saliency position predicts that the rats in these two conditions should display the same amount of contextual fear conditioning. However, if the context facilitation effect depends on rats' storing a conjunctive representation of the specific features of the context, rats in the context same condition should display more contextual fear than do rats in the context shift condition.

The results (Figure 2, bottom) again were consistent with the conjunctive account. Note that the control rats displayed a relatively low level of freezing. Rats in the context same condition displayed enhanced contextual fear, as compared with the rats in the control condition, but rats in the context shift condition did not. So, only the rats that had the opportunity to conjoin the features that made up the conditioning environment (context same) displayed the context facilitation effect. In summary, the two experiments just described cannot be explained by the enhanced saliency view, because it predicts that exposure to the features alone should facilitate contextual fear conditioning. Thus, these results strongly support the idea that rats acquire a conjunctive representation of its features simply as a consequence of exploring a novel environment. This, of course, is the major assumption of the conjunctive account of contextual fear conditioning.

Pattern completion can enhance generalized fear. We now consider a second implication of conjunctive context representations—that the pattern completion afforded by a conjunctive representation can support *enhanced generalized contextual fear* conditioning. Generalized contextual fear conditioning refers to the situation in which conditioning to one context also can be elicited by another context that shares some but not all of the features of the original training context. To appreciate the ability of pattern completion to produce generalized contextual fear, consider the two contexts represented in the top of Figure 3. These two environments were different

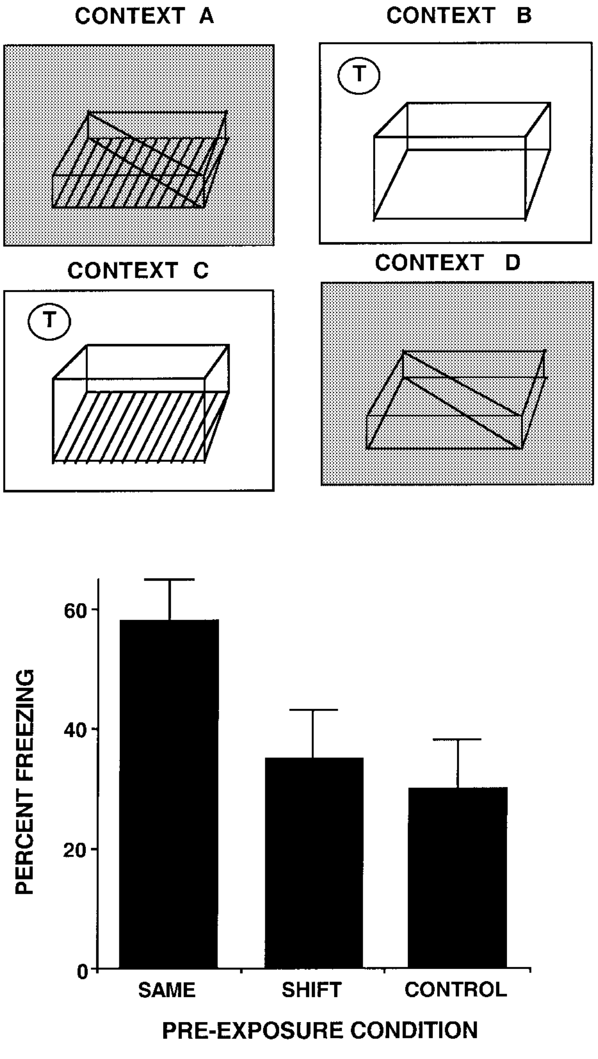

Figure 2. The top of this figure illustrates four contexts used to preexpose rats. The rats in the *same* condition were preexposed to Contexts C and D, whereas the rats in the *shift* condition were exposed to Contexts A and B. The rats in the *control* condition were preexposed to the mouse cage (not illustrated). All the rats were subsequently conditioned in Context C. Differences in shading represent differences in illumination of the ice chests in which the different chambers were placed. The bottom of this figure presents the mean percentage of freezing as a function of the preexposure conditions. Bars represent standard errors of the mean.

but shared several features. Imagine that rats were preexposed to Context A and conditioned to Context B. Preexposure to Context A should establish a conjunctive representation of that context. Because Contexts A and B share several features, it is possible that, during the conditioning session, the features common to both A and B will pattern complete to the representation of A and that the A representation will thus become associated with the shock, in addition to the representation of B. This means that following conditioning to Context B, rats preexposed to Context A will display more generalized fear to A than will rats not preexposed to A.

To test this idea, we preexposed one set of rats to Context A and another set to Context C, which shared no features with Context A or Context B. All the rats were conditioned in Context B. Half of the rats in both preexposure conditions were then tested for contextual fear in the conditioning context, Context B, and half were tested in the generalization context, Context A.

The results of this experiment are presented in the bottom of Figure 3. First, note that the rats in both conditions displayed similar amounts of freezing in the conditioning context (Context B). The rats exposed to Context C, the context that shared no features with the conditioning context, displayed a modest amount of generalized freezing to Context A, but much less than they displayed to the training context, B. In contrast, the rats preexposed to Context A displayed robust generalized fear when tested in Context A. Indeed, they displayed as much generalized fear to the test context as direct fear to the conditioning context, B. These results thus strongly support the implication of conjunctive theory that, via pattern completion, enhanced generalization can be produced.

Nevertheless, there is an alternative, saliency enhancement, explanation of these results. Perhaps as a consequence of preexposure to Context A, the saliency of the features common to B were enhanced and therefore were more strongly associated with shock. Thus, the enhanced generalized fear to A was not due to the network representing A being activated at the time of conditioning but simply to increased conditioning to the common features present in Context B at the time of shock. The implication of this explanation is that preexposure to Context B should enhance generalized fear to Context A as much as

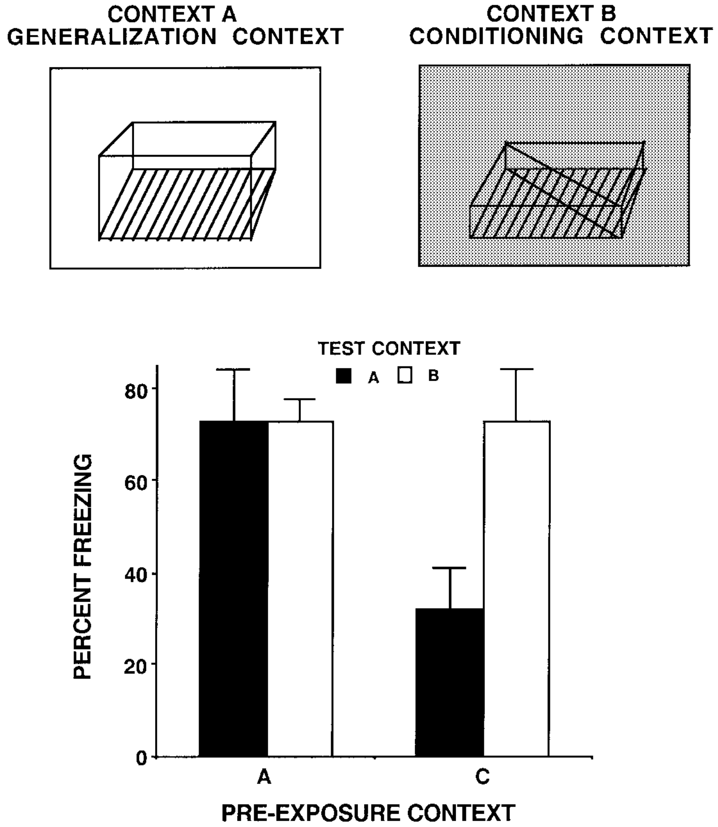

Figure 3. The top illustrates two contexts. All the rats were conditioned in Context B. The rats in one condition were preexposed to Context A. The rats in the other condition were preexposed to a mouse cage (not illustrated). Differences in shading represent differences in illumination of the ice chest in which the different chambers were placed. The bottom of this figure presents the mean percentage of freezing as a function of the preexposure conditions. Bars represent standard errors of the mean.

preexposure to A. This is because, according to the saliency enhancement account, all that matters is that the common features be experienced. The conjunctive representation account, however, predicts that preexposure to B will not enhance generalized fear to A, because the common features can only enhance generalized fear to A if they have become bound with the unique features of A prior to conditioning. As is shown in Figure 4, preexposure to Context A produced enhanced generalized contextual fear to A, whereas preexposure to Conditioning Context B, if anything, reduced generalized fear to Context A. In summary, these two experiments provide strong support for the idea that because a conjunctive representation can support pattern completion, enhanced generalized contextual fear conditioning can be observed.

Pattern completion can support conditioning to a memory representation of a context. We noted that pattern completion afforded by a conjunctive representation is fundamental to explaining why preexposure to context can attenuate the immediate-shock effect. A rat shocked immediately after being placed in the conditioning context shows little or no freezing, because it has not sampled the array of features that make up the context and so cannot be conditioned to them. If the rat is preexposed to the context, however, the network representing the context can be activated by a subset of its features experienced just before shock and thereby support conditioning. There are two assumptions embedded in this analysis that should be made explicit: (1) A subset of features is sampled during the immediate-shock treatment that retrieves or activates the network or memory of the context, and (2) conditioning is to a memory representation of the context.

Fanselow (1990) recognized the importance of the first assumption in his analysis of the immediate-shock effect. He reported that preexposure did not eliminate the immediate-shock effect if the rats indeed were shocked immediately after being placed into the context (see Fanselow, 1986). Facilitation only occurred when the rats were in the context for about 8 sec. Fanselow argued that some time in the context before shock was necessary for a subset of cues to retrieve the context representation.

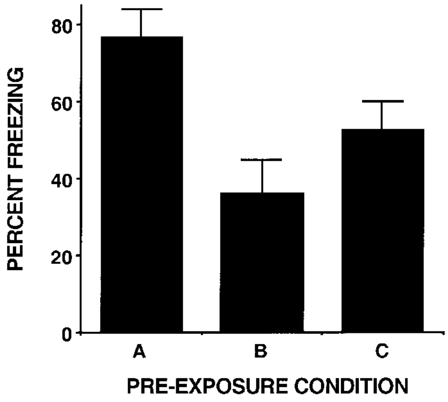

Figure 4. The mean percentage of freezing as a function of the preexposure conditions. Bars represent standard errors of the mean.

If pattern completion to a memory representation of context is responsible for this effect, however, it should be possible to design a preexposure treatment that would facilitate contextual fear conditioning even when the rat is shocked immediately after being placed into the context. To do this, a training procedure is required that ensures that the memory representation of context is active *before the rat is shocked*. The new experiments described below were directed at this issue.

Experiment 1. We used a rather elaborate preexposure treatment designed to attach the representation of the context to the transport cues preceding placing the rat in the context. Because these experiments have not previously been published, we provide more detail about the procedures than was the case for the work just reviewed. Over a 2-day preexposure training session, we exposed adult Long–Evans rats (75–85 days old) to either the conditioning context ($n = 8$) or a control context ($n = 7$) that shared no features with the conditioning context (a mouse cage with a stainless steel top). Each rat received a single 4-min preexposure on the 1st day. On the 2nd day, all the rats were exposed to their respective context four times. Each exposure was approximately 40 sec. The first two exposures and Exposures 3 and 4 were separated by 2 min. A 10-min interval separated Exposures 2 and 3. The rats exposed to the conditioning context were transported from their home cages to the conditioning chamber in a *black ice bucket* that shared no features with the conditioning context. When they were placed into the bucket, the lid was put on so that they could not see where they were being taken. The rats in the control condition were carried to their exposure environment (an opaque mouse cage) in a similar mouse cage. The mouse cage and conditioning chambers were located in different rooms. The intent of these multiple exposures was to establish the features of the black bucket as retrieval cues that would activate the representation of the context. So, as the rat was being transported to the conditioning room (which required about 15 sec), the bucket should have activated the representation of the context. If successful, this procedure should result in considerable contextual fear conditioning even when rats are shocked immediately after being placed into the context, because the context representation is activated at the time the rat is shocked.

On the conditioning day, all the rats experienced one additional preexposure trial. Two minutes later they were brought to the conditioning context in their respective carrying cage (black bucket or mouse cage), placed in the conditioning chamber, and *immediately shocked* (2 sec, 0.6 mA). Approximately 24 h later, each rat received the contextual fear test.

The results of this experiment are shown in the top of Figure 5. Note that the rats in the control condition displayed the immediate-shock effect. They showed essentially no freezing. In contrast, the rats given multiple

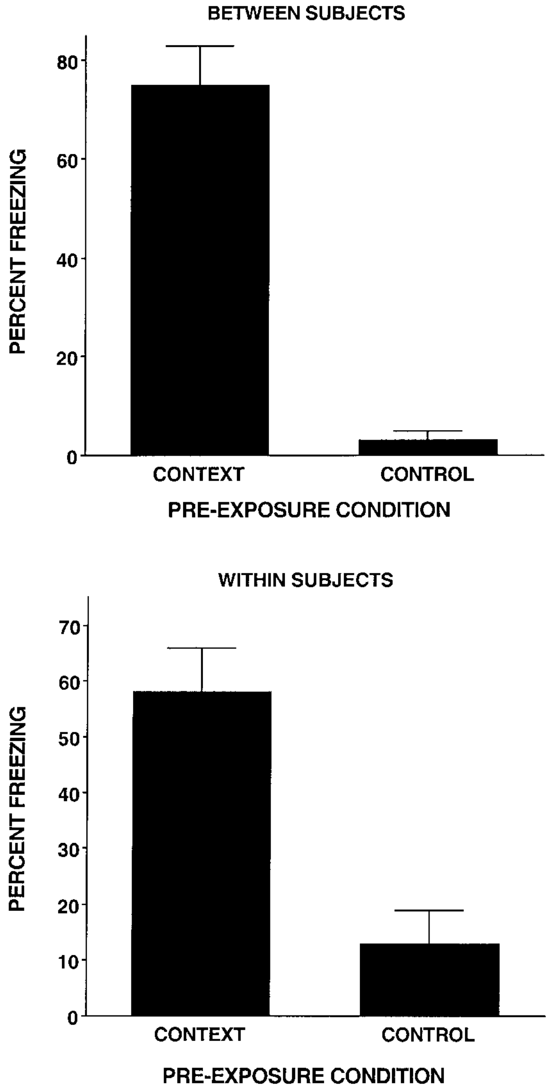

Figure 5. The mean percentage of freezing as a function of the preexposure conditions. Bars represent standard errors of the mean. The top of this figure presents the results of the between-subjects experiment described as Experiment 1 in the text. The bottom presents the results of the within-subjects experiment described as Experiment 2 in the text.

preexposures to the conditioning context displayed significantly more freezing than did the control animals [$F(1,13) = 12, p < .005$].

Experiment 2. These results suggest that multiple preexposures established the black bucket as a retrieval cue that could activate the conjunctive representation of the context. To ensure that this was the critical feature of the experiment, we repeated this experiment but gave all the rats *both* preexposure treatments: During preexposure training, each rat was carried in the black bucket and placed in the conditioning chamber, Context A, and each rat was carried in a mouse cage and placed into the mouse cage control environment, Context C. Over 2 days, each rat was exposed seven times to each environment. The first exposure to each was for 4 min. Thereafter, it was for approximately 40 sec. The rats were given three exposures to each environment on Day 1, and four exposures to each on Day 2. The exposure sequence to A and C and the time interval separating exposures in parentheses on Day 1 was A (15 min), C (4 h), A (15 min), C (15 min), C (15 min), A. On Day 2, the sequence was A (15 min), C (15 min), C (15 min), A (15 min), C (15 min), A (15 min), (15 min), A. On the conditioning day, each rat was brought into the conditioning chamber and shocked immediately. The rats were carried to the conditioning chamber in either the black bucket ($n = 8$) or the mouse cage ($n = 7$).

Note that this procedure ensured that each rat had the opportunity to acquire the conjunctive representation of the context. However, it uniquely established the black bucket as a retrieval cue to activate the representation of the context. Thus, from the pattern completion account, one would expect that the rats brought to the conditioning chamber in the black bucket should display much more contextual fear conditioning following immediate shock than rats brought to the conditioning context in the mouse cage. As is shown in the bottom of Figure 5, the rats brought to the chamber in the mouse cage (labeled *control* in Figure 5) showed the immediate-shock effect—they displayed very little freezing. In contrast, the rats brought to the conditioning context in the bucket (labeled *context* in Figure 5) displayed markedly more freezing [$F(1,13) = 13, p < .005$].

These results are consistent with the primary premise of the conjunctive representation view and strongly encourage the belief that, as a consequence of preexposure, rats have established a memory representation of context that can support conditioning if it is activated, presumably via pattern completion, at the time shock occurs.

Experiment 3. There is, however, an even stronger way to evaluate this position. The implication of these data and the theory that guided the experiments is that the physical cues present at the time of shock are less important for the development of conditioned fear than is the memory representation that is active at that time. Indeed, if our interpretation is correct, the rats were conditioned to the memory representation activated by the transport environment, not to the physical cues present at the time of shock. To test this idea in its extreme form, we established a transport–context association through preexposure and then used this transport to bring rats into a *different* context for immediate-shock conditioning. We then tested the rats in either the original, associated context or the actual conditioning context. If the rats were to display freezing in the original associated context and not in the actual conditioning context, this would be strong support for the idea that the rats were conditioning to the memory representation active at the point of shock, and not to the physical cues.

The rats were preexposed to one of two contexts displayed as Context A or Context B in Figure 6. Context A was composed of a large transparent Plexiglas chamber that sat on a smooth Plexiglas floor inside an Igloo ice

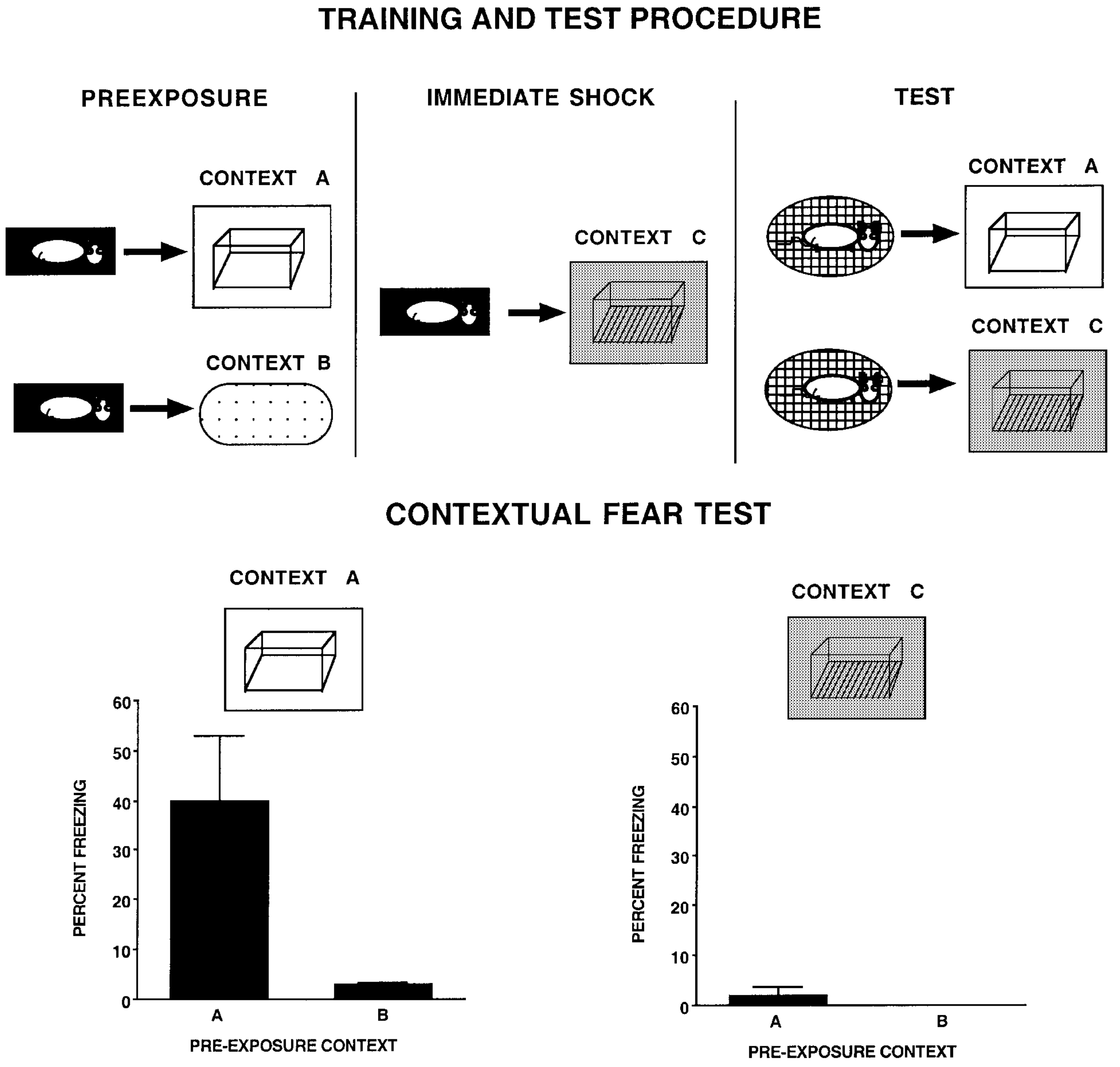

Figure 6. The top of this figure illustrates the three phases of Experiment 3. The black rectangle represents the black bucket. During preexposure, different rats were preexposed to either Context A or B (a mouse cage). For the immediate-shock conditioning, all the rats were transported to Context C in the black bucket. Half the rats from the two preexposure conditions were tested in Context A, and half were tested in Context C. Note that they were transported to the test context in a perforated metal pan. The results of the contextual fear test are presented in the bottom of this figure as the mean percentage of freezing as a function of the preexposure conditions. Bars represent standard errors of the mean. Freezing in Context A is presented on the left, and freezing in Context C is presented on the right.

chest that had a white interior (the same context used in the previous two experiments). It was illuminated by a 6-W AC light bulb. The door to the ice chest remained open throughout the experiment. Context B was a mouse cage with a metal top. The rats were given multiple exposures (nine) to either Context A or Context B distributed over 2 consecutive days (four on Day 1 and five on Day 2). The rats were transported to the exposure context in the black bucket. The first exposure was 4 min; thereafter, all exposures were approximately 40 sec. On Day 2, between Preexposure Trials 3 and 5, each rat also was placed twice (for 2 min) into a perforated metal pan that was part of a balance scale used to weigh the rats.

On Day 3, the rats were conditioned. They were taken from their home cage in the black bucket, placed in Context C, and shocked immediately. Note that Context C was designed to be very dissimilar to Context A. There was no illumination in the room, and the chamber was small and rectangular. It sat on a grid floor that permitted the delivery of footshock. The chamber was inside the Igloo ice chest, but it was illuminated minimally with red light, just enough to permit the experimenter to put the rat in the chamber, to deliver shock, and to score freezing during the test. The day following conditioning, the rats from each condition were tested for fear of the shock, Context C ($n = 8$), or for fear to Context A ($n = 8$). To ensure that any freezing during the test was not due to conditioning to the transport cage that spread to the conditioning context, we transported the rats to the conditioning chamber in the open metal pan (see Bevins & Ayres, 1995; Bevins, Rauhut, McPhee, & Ayres, 2000).

Because the rats had not been exposed to Context C and were shocked immediately, there should be no fear conditioned to it. However, if, as is implied by conjunction theory, rats can condition to the memory representation of context, then the rats that had been preexposed to A should display substantially more fear to Context A than the rats who had been preexposed to Context B. Moreover, the rats preexposed to Context A and tested in Context A should display more freezing than the rats preexposed to Context A and tested in Context C (the place where the rats were conditioned).

As can be seen in Figure 6, the rats apparently were conditioned to the memory of the representation of Context A. Neither group displayed freezing in the conditioning context, C. This is the immediate-shock effect. When tested in Context A, however, the rats that had been exposed to Context A displayed significantly more conditioning than did the rats preexposed to Context B [$F(1,14) = 18$, $p < .001$]. It is especially important to appreciate that the rats preexposed to Context A displayed much less freezing when they were tested in Context C, the conditioning context, than when they were tested in Context A. This observation rules out the possibility that conditioning to Context C generalized to Context A. Evidently, the rats were conditioned to a memory representation of a previously experienced context failed to condition to the environment in which the shock occurred. This observation thus provides strong support for the conjunctive representation view of context.

Summary. We have explored some of the implications that the conjunctive representation has for contextual fear conditioning. Consistent with this view, we have provided evidence that, just by exploring the context, the normal rat automatically stores a conjunctive representation of its features. This representation, via its ability to support pattern completion, can lead to enhanced generalized contextual fear and mediate fear to the memory representation of context. These results provide strong support for the idea that rats acquire a conjunctive representation of the context.

Computational Simulations

The theoretical principles behind our account of the division of labor between the hippocampus and the cortex have been implemented in a computational neural network model, which reproduces a wide range of learning and memory phenomena in rats (O'Reilly & Rudy, in press). For example, the model captures the pattern-completion-based contributions of the hippocampus in two of the main fear conditioning results summarized previously: preexposure-mediated elimination of the immediate-shock effect and the generalized fear effects. Here, we show that this same model also captures the ability of the rat to condition to a memory representation of a context, as was demonstrated in Experiment 3 above. In addition to showing that this result is consistent with the concrete implementation of our theoretical principles, the model makes the strong prediction that this ability to condition to the memory of context is dependent on the hippocampus.

We refer the reader to O'Reilly and Rudy (in press) for the details of the computational model and just summarize the key principles here. The overall structure of the model (Figure 7) includes a stimulus input representation that the network learns to map to a corresponding output representation. In the case of fear conditioning, this output represents an expectation of shock (i.e., fear) or expectations of other outcomes. Mediating this input–output

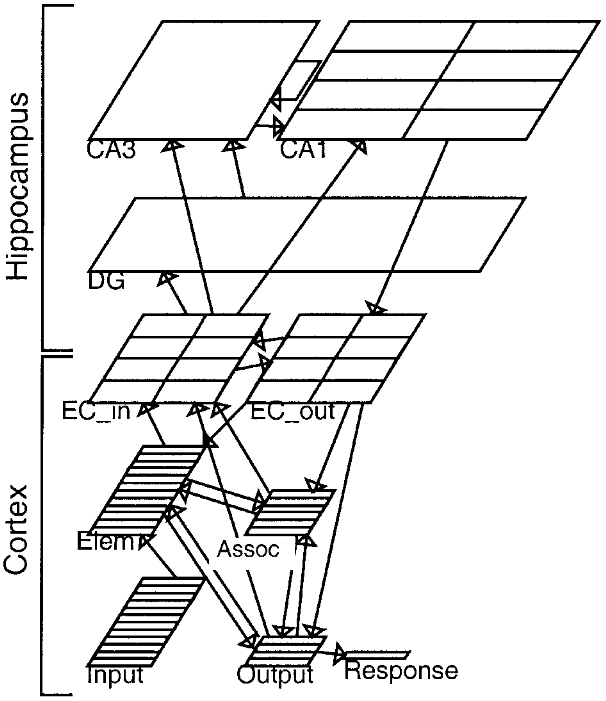

Figure 7. The O'Reilly and Rudy (in press) model of hippocampal–cortical circuitry. The cortex has 12 different input dimensions (sensory pathways), with four different values per dimension. These dimensions and values are represented separately in the elemental cortex (Elem). The higher level association cortex (Assoc) can form conjunctive representations of these elements, if demanded by the task. The interface to the hippocampus is via the entorhinal cortex (EC), which contains a one-to-one mapping of the elemental, association, and output cortical representations. The hippocampus can reinstate a pattern of activity over the cortex via the EC.

mapping are three different levels of connections. At the lowest level, there is an *elemental* cortical representation that just encodes the stimulus features in a one-to-one (separate, elemental) fashion and has modifiable weights to the outputs. This allows for features-based associations, as was discussed above. In addition, the cortex in our model also has an *association* area, which receives from the elemental inputs and can learn conjunctive representations thereof. However, this cortical area is not biased to learn these conjunctions and only learns them slowly and under pressure from task demands via error-driven learning mechanisms. The third level is the hippocampus, which receives from the entire cortex in the model and sends to the output layer. The simulated hippocampus captures the basic neuroanatomical structure of the rat hippocampus, and has sparse activations to produce a strong bias for learning conjunctive representations (Marr, 1971; O'Reilly & McClelland, 1994). Thus, this hippocampal area will naturally and automatically encode conjunctive representations of the input features presented to it.

To simulate Experiment 3, we first presented the model with preexposure stimuli, as is shown in Figure 8 (top row). The first stimulus represents the black bucket transport, which is always followed by Context A. The activations of the model persist between these two events, with the result that a common hippocampal representation develops that encodes both the transport and Context A together. In this simulation and the original preexposure simulations in O'Reilly and Rudy (in press), 100 trials of preexposure training were run, where each trial represents the equivalent of one fixation of a set of visual features and the learning that takes place as a result of processing those features. To condition the model, we present the patterns shown in Figure 8 (bottom row), which include the shock association, as patterns over the output layer of the model. This represents the bucket followed by the novel conditioning environment (C), which has the shock input activated (left-hand column of the output layer). After a single conditioning trial, the model was tested with Context A (the preexposure context), and Context C (the actual conditioning context). We ran this simulation with both an intact model and a model with the hippocampus removed.

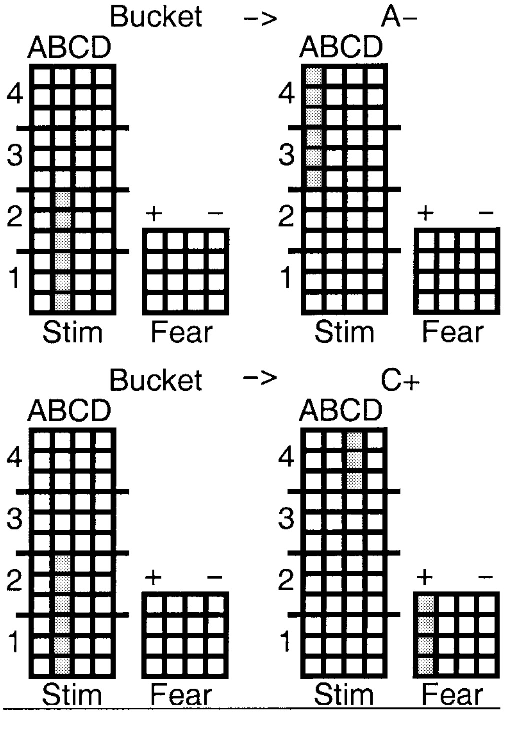

Figure 8. Training patterns for simulating Experiment 3 in the model. The top row shows the preexposure training, where the features for the black bucket (in column B) are activated, followed by the features for the Preexposure Context A (in column A). The bottom row shows the features used for shock conditioning. The bucket representation was activated again, followed by novel features for the conditioning chamber (Context C, in column C). Note that Context C has fewer features to capture the fact that it was dark in the experiment. If a larger number of features are used, the conditioning result remains but is slightly diminished in magnitude.

The results of this simulation are displayed in Figure 9. The dependent variable in this figure (fear response) is the average activation over the shock output units of the model generated by Context A and Context C. This figure reveals two important results. (1) With the intact model, Context A, the preexposed context generated more fear than did Context C, the actual conditioning context. This is the same result as that found in the actual behavioral experiment. (2) Removal of the hippocampal component of the model eliminated the benefits of preexposure, and neither Context A nor C generated a fear response. Thus, our model correctly predicts the pattern of results observed in Experiment 3. It also predicts that rats with damage to the hippocampus will not display the benefits of preexposure. Thus, these results support our general view that the hippocampus is critical for encoding a conjunctive representation of context and for supporting pattern completion of these conjunctive representations.

General Discussion

The goal of this paper was to elaborate on a dual-representation view of how the brain represents context and to explore this view in the context of hippocampal contributions to contextual fear conditioning processes. In the spirit of Nadel and his colleagues (Nadel & Willner, 1980; Nadel et al., 1985), our position is that either context can be represented as a set of independent features (the features representation view) or these features can be bound into a unitary encoding that represents their cooccurrence (the conjunctive representation view). We assume that extrahippocampal areas provide a basis for feature representations and that the hippocampus makes an essential contribution to the encoding of conjunctive representations. However, we constrained the latter idea by distinguishing between (1) conjunctive representations that are acquired rapidly and automatically as a result of

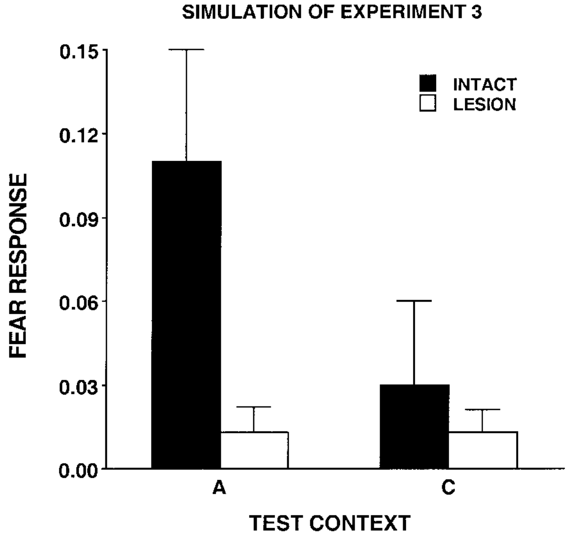

Figure 9. Simulation of Experiment 3: Conditioning results measured in the model for the preexposure context (A) versus the actual conditioning environment (Context C). The dependent measure is average activation over the shock/fear units in the output layer. *N* = 25 different random weight initializations. The model shows conditioning to the Preexposure Context A, which was not present during actual conditioning, whereas the actual conditioning environment was not conditioned.

the subject's exploring its environment and (2) conjunctive representations that are gradually acquired and must be learned in order for a problem to be solved. The hippocampus, in our view, makes an essential contribution to conjunctions that are learned automatically.

A key property of hippocampal-dependent conjunctive representations is that they provide a mechanism for pattern completion, where a subset of a stored pattern (conjunction) can activate the entire pattern. We interpret the impaired contextual fear conditioning following damage to the dorsal hippocampus as resulting from impaired conjunctive pattern completion. Damage to the hippocampus, however, may not always result in impaired contextual fear conditioning, presumably because fear conditioning can also be supported by hippocampus-independent feature representations. Because there are at least two systems that can support contextual fear conditioning, detailed parametric studies will have to be done to completely understand the factors that determine the role of the hippocampus and other structures in contextual fear conditioning.

Although the hippocampal lesion literature is complex, there can be little doubt that simply as a consequence of exploring a context, a rat stores a conjunctive representation. We have shown two particularly interesting results of this phenomenon, where preexposure can result in enhanced generalized fear (Rudy & O'Reilly, 1999) and can lead to conditioning to memory representations of context (Experiments 1, 2, and 3). That rats will display more conditioning to the activated memory of a context than to the actual place where shock was experienced appears to demand the operation of the pattern completion mechanism afforded by a conjunctive representation. Exploring how damage to the hippocampus affects these interesting phenomena associated with context preexposure should establish the role of the hippocampus in storing conjunctive representations.

One advantage of our theoretical position is that it reveals previously unrecognized relationships between processes embedded in contextual fear conditioning and those operating in other domains, such as the study of habituation and incidental learning. There is an emerging literature indicating that rats automatically store conjunctive representations in a number of such tasks and that the hippocampus makes an important contribution to these phenomena (e.g., Good & Bannerman, 1997; Good & Honey, 1991; Honey, Watt, & Good, 1998; Save, Poucet, Foreman, & Buhot, 1992). They include studies of the habituation of exploratory behavior (Save et al., 1992), habituation of the orienting response (Honey et al., 1998), and the context specificity effect observed in Pavlovian conditioning (Good & Bannerman, 1997; Good & Honey, 1991). These studies all provide evidence that animals automatically store representations of stimulus conjunctions, even though there is nothing about these tasks that require this learning. The incidental conjunctive learning was revealed by transfer tests that occurred following training, in which the relationship among the features was varied. These studies also show that this learning depends on the hippocampus. An obvious implication of our theoretical analysis is that the context preexposure effects we have described should also require a contribution from the hippocampus. We are currently evaluating this prediction.

We also have discussed the relationship of our position to other theories of hippocampal function (O'Reilly & Rudy, in press; Rudy & O'Reilly, 1999), so we will only highlight several key relationships here. At a general level, our view has much in common with the ideas O'Keefe and Nadel (1978) put forth. They assume that the hippocampus makes an essential contribution to a *locale system* that supports cognitive maps and that a hippocampal-independent *taxon system* supports other types of habits. Our view of hippocampus-supported conjunctive learning goes beyond the learning of spatial relationships among features of the environment that is the basis of O'Keefe and Nadel's cognitive mapping theory. The key point of contact with our position is that they also assume that these two systems differ on other dimensions. Two that relate to our view are (1) *learning rate*, where the locale system is viewed as rapidly storing new information, whereas the taxon system learns and unlearns by slow increments, and (2) *motivation*, where the two systems operate under different motivational conditions. The locale system is fundamentally connected to exploration, and much of what it stores occurs as a result of novelty-directed behavior. Taxon learning, however, is motivated to function in the service of problem solving or achieving goals. It is therefore sensitive to the reinforcement contingencies associated with behavior.

We embrace similar ideas in distinguishing between our hippocampal-dependent conjunctive system and the neocortical learning system (see O'Reilly & Rudy, in press).

The idea of the hippocampal formation as a rapid automatic storage device appeared early in the history of theorizing about the hippocampus (e.g., Marr, 1971). It is also present in contemporary views (e.g., McNaughton & Nadel, 1987; Morris & Frey, 1997; Squire, 1992). Some other models of hippocampal function, however, do not appear to be consistent with the incidental role of hippocampal learning, since they posit that the hippocampus is uniquely responsible for error-driven learning (Gluck & Myers, 1993; Schmajuk & DiCarlo, 1992). These models are also inconsistent with the idea that the cortex is capable of powerful, error-driven conjunctive learning in the absence of the hippocampus. Nevertheless, they do endorse the idea that the hippocampus is important for learning higher order conjunctive representations.

In this paper, we have focused on recent issues that have emerged in the study of the neurobiology of contextual fear conditioning. It is appropriate to note, however, that the basic ideas and issues that we have considered originated in the study of discrimination learning (see Rudy & Wagner, 1975). The fundamental issue is to conceptualize how the organism represents a stimulus compound. Is it represented as a set of independent elements or features (e.g., Spence, 1936, 1937), or is it represented as a configuration (e.g., Gulliksen & Wolfle, 1938)?

Elemental theorists assume that associations are to the independent, feature representations of the compound. These theories have proven to be extremely powerful in their ability to explain a range of phenomena observed when conditioning procedures involve compound stimuli. For example, the influential Rescorla–Wagner model of Pavlovian conditioning (Rescorla & Wagner, 1972) assumes an elemental representation of compound cues. It has had remarkable success in accounting for a wide range of conditioning phenomena involving compounds, such as blocking (Kamin, 1968), conditioned inhibition, and the cue-validity effect (Wagner, Logan, Haberlandt, & Price, 1968). However, their basic model was unable to account for the fact that animals solve nonlinear discriminations that demand a configural/conjunctive representation of the stimulus environment, problems such as negative patterning (Rescorla, 1972; Whitlow & Wagner, 1972; Woodbury, 1943), or the biconditional discrimination problem (Saavedra, 1975). So, they granted that configural representations must exist and are capable of controlling behavior. However, they also assumed that configural representations do not compete well with the elemental representations of their components for associative control of behavior and gain control only when the task demands their use (see Rescorla, 1972: Whitlow & Wagner, 1972). They represented this position in their model by assuming that the configural cue has low saliency and will be conditioned to very slowly, as compared with its elemental components.

More recently, Pearce (1987, 1994) has become the major proponent of configural theory. He has argued that animals always (automatically) construct a configural representation of stimulus compounds and has shown how this view can account for a wide range of phenomena, including blocking, conditioned inhibition, nonlinear discrimination, and generalization among the cues of a compound.

It is interesting to compare the basic assumptions of our computational neural network model (O'Reilly & Rudy, in press) with these two theoretical positions—one that assumes that configural representations only come into play when the task demands their use (Rescorla, 1972; Whitlow & Wagner, 1972) and the other that assumes that configural representations are automatically constructed and play a dominant role in associative learning. We assumed that it is the role of the hippocampus to rapidly and automatically construct representations of stimulus conjunctions but that, in the absence of the hippocampus, the cortex alone can gradually construct stimulus conjunctions if forced to by the demands of the task. So, in effect, our position captures both views but assigns them to different brain systems.

We end this discussion by reiterating the significance of pattern completion processing supported by hippocampal-dependent conjunctive representations. We have noted that Squire (1992) suggested that pattern completion is at the heart of declarative memory (see also Tyler & DiScenna, 1986). We support this view and emphasize that pattern completion provides an important bridge for linking the memory processes that support declarative memory in people with memory processes operating in animal models. A major characteristic of human declarative memory is that it supports the conscious recollection of memory. Animals other than people might be able to consciously recollect, but we have no way of knowing this. Thus, it is impossible to point to an animal model of this feature of declarative memory. However, as has been discussed extensively in this paper, we do know how to study conjunctive representations and pattern completion in other animals. Therefore, if pattern completion processes are critical to human declarative memory, we should be able to understand a great deal about human declarative memory by studying basic pattern completion mechanisms in animals.

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