

Contextual Fear Conditioning, Conjunctive Representations, Pattern Completion, and the Hippocampus

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Impaired contextual fear conditioning produced by damage to the hippocampus has been attributed to the loss of a conjunctive representation of the features of the context. There is, however, no direct evidence that conjunctive representations contribute to contextual fear conditioning. These experiments addressed this issue and found support for the conjunctive representation view. Two results made this point: (a) Preexposure to the conditioning context, but not to its separable features, facilitated contextual fear conditioning, and (b) generalization of fear conditioning to similar contexts was enhanced by preexposure to the context used to test for generalization. These results are interpreted as pattern completion to the preexposed context during the conditioning episode. They support the view that a conjunctive representation of context plays an important role in contextual fear conditioning and that the impairments produced by damage to the hippocampus result from the loss of this conjunctive contribution.

The environmental and temporal context in which a learning episode occurs can be an important part of what is represented about that episode. On both neurobiological and psychological grounds, one can argue for a dual representation of the learning context. Context can be represented as (a) a collection of independent feature elements (the *elemental* context representation) and/or (b) a binding together of these independent features in a representation of their conjunction (the *conjunctive* context representation). These ideas were laid out and elaborated several years ago in articles by Nadel and Willner (1980) and Nadel, Willner, and Kurtz (1985). For example, Nadel et al. proposed that cues of the environment (context) are represented in the neocortical systems “simply as things that have certain features and these representations provide one means by which cues can be associated with each other” (pp. 393–394). The elaboration of elemental features into a representation of stimulus conjunctions, however, is widely believed to depend on both the neocortex and its interactions with the hippocampus. Nadel et al. referred to these elaborated representations as cognitive maps (see also O’Keefe & Nadel, 1978). Other researchers have referred to them as configural representations (Sutherland & Rudy, 1989), unitary representations (Fanselow, DeCola, & Young, 1993), or representations of stimulus conjunctions (McClelland, McNaughton, & O’Reilly, 1995).

One important source of evidence that appears to support a role for the hippocampus in the representation of context is the contextual fear conditioning literature. When a rat experiences pairings of a discrete auditory cue and aversive shock, it will display fear (as measured by freezing) to both

the auditory cue and to the context in which the tone–shock pairings occurred. Several researchers have reported that damage to the hippocampus impairs contextual but not auditory-cue fear conditioning (Anagnostaras, Maren, & Fanselow, 1999; Kim & Fanselow, 1992; Kim, Rison, & Fanselow, 1993; Logue, Paylor, & Wehner, 1997; Phillips & LeDoux, 1992, 1994; Selden, Everitt, Jarrard, & Robbins, 1991; Young, Boheneck, & Fanselow, 1994). Consistent with Nadel et al.’s (1985) proposal, some researchers have suggested that the dependence of contextual fear conditioning on the hippocampus is due to the fact that the rat can no longer construct a unitary, conjunctive representation of the collection of cues that form the context (e.g., Fanselow et al., 1993; Fanselow & Rudy, 1998; Maren, Aharonov, & Fanselow, 1997; Rudy & Sutherland, 1992, 1994, 1995).

However, what has been lacking in the literature is strong evidence that rats with an intact hippocampus actually construct a conjunctive representation of context, as compared with context having its effect by means of elemental representations. The primary importance of the experiments described in this article is that they provide compelling evidence that a conjunctive representation makes a significant contribution to contextual fear in the normal rat. Thus, this evidence substantiates the interpretation that impaired contextual fear conditioning produced by damage to the hippocampal formation is due to the loss of the conjunctive, not elemental, representations of context.

To understand why the existing literature does not directly support the idea that the hippocampus constructs conjunctive context representations, we first examined the basic finding that hippocampal lesions reduce or eliminate contextual fear. This finding suggests a role for the hippocampus in the representation of context but does not specifically indicate that the context is represented in a conjunctive manner. Indeed, given that the subject can sense the independent features of the context, it is surprising that representations of these features are not associated with shock to support contextual fear conditioning.

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Why should a conjunctive representation of context support more conditioning than the unconjoined features? One argument is that contextual fear conditioning should be more robust if it is based on a conjunctive representation because, during testing, such a representation could be activated by a subset of the features that make up the context. Thus, the level of fear expressed would be a function of the amount of conditioning to the entire network of features, not just to the individual ones that happen to be sampled during testing (Kiernan & Westbrook, 1993). It has also been suggested that in the normal rat, the conjunctive representation system dominates the elemental representation systems (Maren et al., 1997).

Although these explanations for the role of the hippocampus in contextual fear conditioning are interesting, there is little if any direct evidence that uniquely supports these views. Some consistent evidence came from Fanselow's (1990) analysis of what is called the *immediate shock effect*. If animals were given a single strong shock immediately after being placed in the conditioning chambers, they failed to show fear of the conditioning context when tested 24 hr later. However, they did show fear if they were in the conditioning chamber for about 30–60 s before being shocked. Fanselow suggested that animals in the immediate-shock group failed to condition because they did not have time to encode the conjunctive representation of the conditioning context before the shock occurred. He provided support for this interpretation by showing that a 2-min exposure to the context 24 hr before conditioning enhanced the level of contextual fear conditioning exhibited by rats who were shocked shortly after being placed into the context. Presumably, this exposure was sufficient to permit the rats to construct the unitary, conjunctive representation of the context needed for conditioning when shock occurred shortly after placement in the chamber.

Fanselow's findings have been replicated and extended by Westbrook and his colleagues (Kiernan & Westbrook, 1993; Westbrook, Good, & Kiernan, 1994), and, as noted above, Kiernan and Westbrook (1993) have proposed that it is the integrated (conjunctive) neural network representation of context that supports fear conditioning. There are also a number of other reports that prior exposure to the context can facilitate subsequent contextual fear conditioning (Pugh, Tremblay, Fleshner, & Rudy, 1997; Rudy, 1996; Rudy & Morledge, 1994).

That prior exposure to the conditioning context can facilitate contextual fear conditioning is consistent with the view that rats learn about the features of a context independent of associating these features with shock (Fanselow & Rudy, 1998). However, it does not necessarily follow from these results that during preexposure the rat actually acquires a conjunctive representation of the context. For example, it might be that preexposure strengthens the representations of the independent feature elements of the context, thereby increasing their saliency and allowing each feature to be more easily associated with the shock.

Thus, in this article, we attempt to distinguish between two alternative explanations for why preexposure facilitates contextual fear conditioning. The *saliency enhancement*

view, just described, argues that animals learn about each feature of the context independently of the other features (i.e., using an elemental representation), whereas the *conjunctive representation* view argues that it is the specific conjunction of cues that is represented.

We used two approaches to evaluate these views. In one case, we designed experiments that compared the effects of preexposure to the conditioning context with preexposure to the individual feature elements of the context. The saliency enhancement view predicts that these two preexposure treatments should have similar effects on subsequent contextual fear conditioning. The conjunctive representation view predicts that preexposure to the context (i.e., the conjunctions of the features) will have different effects than preexposure to the individual features.

The second strategy was designed to evaluate another implication of the conjunctive representation view. According to this view, the memory of an input pattern can be activated by a subset of the original cues. This is called *pattern completion* (Marr, 1971; McNaughton & Morris, 1987; O'Reilly & McClelland, 1994), and it has been viewed as central to what is sometimes referred to as declarative memory (Squire, 1992). In these experiments, we attempted to provide evidence for pattern completion by exploring the generalization of contextual fear conditioning based on preexposure to contexts that are similar, but not identical, to the conditioning context.

By specifically trying to rule out the saliency enhancement interpretation of preexposure effects on contextual fear conditioning in intact rats, we provide support for the notion that animals learn a conjunctive representation of context. Furthermore, our experiments show that intact rats exhibit properties that would only be expected of conjunctive representations (i.e., pattern completion). By providing support for the conjunctive view, one can make a stronger case for interpreting impaired contextual fear conditioning produced by damage to the hippocampal formation as being due to the loss of conjunctive representations.

General Method

Subjects

Subjects were Long-Evans-derived, hooded rat pups born to dams bred at the University of Colorado. Litters were culled to 9 pups (5 males and 4 females) on Postnatal Day 1, and pups were weaned when 21 days old. The rats were maintained on a 12-hr light–dark cycle. Preexposure, conditioning, and testing occurred between 7:00 and 10:30 a.m. At 35 days old, rats were sexed and housed in same-sex groups of 4 to 5 subjects.

Apparatus

Conditioning occurred in two identical Igloo ice chests (54 cm long \times 30 cm high \times 27 cm deep) with white interiors. A clear plastic window (30 \times 18 cm) was cut into the door of each chest so that the rats could be observed. Inside the chest was one of two different chambers that were used to enclose the rat. The four sides of each chamber were constructed of transparent Plexiglas, and the tops were made of wire-mesh screen. One chamber was relatively large (26 cm long \times 21 cm wide \times 24 cm high) and rectangular in

shape. The other was relatively small (26 cm long \times 21 cm wide \times 10 cm high) with a triangular interior (see Figure 1). The triangular interior was created by connecting two diagonal corners with a transparent Plexiglas panel (34 cm \times 10 cm). During a conditioning session, the chamber sat on a removable, stainless steel rod floor used to deliver the unconditioned stimulus (US), a 2-s, 0.4-mA shock. The rods were 1.5 mm in diameter and were spaced 1.2 cm center to center. Each rod was wired to a shock generator and scrambler (8240415-SS, Lafayette Instruments Lafayette, IN). The rods and floor of each chamber were cleaned before each rat was trained or tested.

Conditioned fear was assessed by measuring conditioned freezing—the rat's natural defensive response to anticipated danger. During the contextual fear test, rats were placed into a conditioning chamber and observed for 5 min. Every 10 s, a time-sampling procedure was used to judge each rat as either freezing or active, at the instant the sample was taken. *Freezing* was defined as the absence of visible movement except for respiration. In our laboratory, the correlation between observers exceeded .95. At the time of testing, the observer had no knowledge of the subject's treatment condition.

Experiment 1

To decide between the saliency enhancement versus the conjunctive representation views of the context preexposure effect, we compared the performance of three groups of rats given different preexposure experiences. Rats in the *context* preexposure group were exposed to the conditioning context. Rats in the *features* exposure group were exposed to the independent features of the conditioning context, but these features were not experienced together. Rats in the *control* group were preexposed for a comparable period to a context that shared no features with the conditioning context, an opaque mouse cage. The saliency enhancement view of context learning predicts that preexposure to either the context or to its features should facilitate the expression of

contextual fear conditioning. In contrast, the conjunctive representation view predicts that rats preexposed to the context should display significantly more contextual fear than rats exposed to the features separately.

The assessment of preexposure effects used in this experiment was based on a finding reported by Rudy and Morledge (1994) that is similar to the preexposure effects on immediate shock learning discussed above. They tested young rats for contextual fear conditioning at different retention intervals and found that during a period ranging from 10 min to 3 hr, rats displayed reduced fear compared with rats tested 24 hr after training. Rudy and Morledge suggested that the reduced contextual fear conditioning occurred because there is a lengthy consolidation period for constructing a conjunctive representation of the context, and until this representation is established, the conditioning context will be less effective in retrieving the representation of shock. Consistent with this idea, they reported that the reduced contextual fear at the short retention interval could be eliminated by preexposing the rats to the context 24 hr before conditioning.

Presumably, Rudy and Morledge's result occurred because preexposed rats had consolidated a conjunctive representation of context that was available at the time of conditioning and testing. As noted, however, one could also argue that preexposure produces learning that enhances the saliency of the independent features of the context.

Method

The subjects were 34 male rats that were 30 days old at the start of the experiment. They were randomly assigned to three groups ($n_s = 10, 12, \text{ and } 12$). Four exposure environments were constructed that contained features from the conditioning context (see Figure 1). Context A was the conditioning context, which consisted of the large rectangular chamber placed on the rods used to deliver shock. This chamber was placed inside the sound-attenuating ice chest, which was illuminated by a 6 W, clear bulb. Three other environments (Contexts B, C, and D) were constructed to expose rats to the independent features of the conditioning context. Context B consisted of the small triangular chamber placed on the rod floor in the animal colony room (Room A). Context C was a transparent mouse cage (26 cm long \times 16 cm wide \times 12 cm high) placed inside the illuminated ice chest, thus exposing the rats to the chest's interior. Context D was the large Plexiglas chamber, which sat on a Plexiglas floor on a bench in the central laboratory room. (Room B). Context E was an opaque mouse cage (26 cm long \times 16 cm wide \times 12 cm high). It had no features in common with the conditioning context and was located in the central laboratory room.

Approximately 24 hr before conditioning, rats in the context condition were exposed for 4 min each to Context A and Context E. Preexposure began with the 4-min exposure to Context A and was followed by two 4-min exposures to Context E. Rats in the features exposure group were exposed for 4 min each to Contexts B, C, and D. Rats in the control condition were exposed three times to Context E. Each exposure was separated by 30 min. On the day of conditioning, the rat was placed into the conditioning chamber (Context A) and 120 s later received a 2-s, 0.4-mA shock. The rat was then returned to the home cage for 10 min and brought to the conditioning room, where it was tested for 5 min.

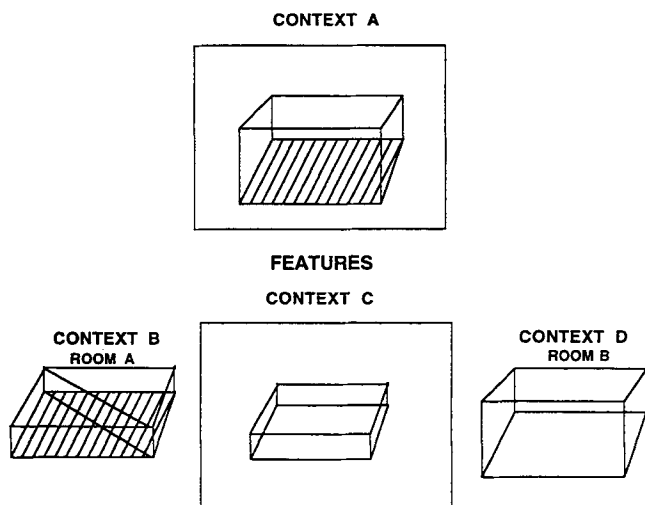


Figure 1. Illustration of the four contexts used to preexpose rats in the context and features conditions of Experiment 1. The conditioning context was a rectangular Plexiglas chamber placed inside an ice chest. This context was then decomposed into features that rats in the features condition experienced separately.

Results and Discussion

As shown in Figure 2, there were large differences between the groups, $F(2, 32) = 13.80$, $p < .001$. As expected, rats in the control condition displayed very little contextual fear conditioning. Rats in the features condition also displayed very little fear. In contrast, preexposure to the conditioning context significantly increased the rats' contextual fear conditioning. Post hoc Newman-Keuls tests confirmed that rats preexposed to the context were significantly different from rats in the other groups ($p < .01$). No other differences were reliable.

Rats in the context and features conditions were exposed equally to the features of the conditioning context, but only rats exposed to the conditioning context displayed facilitated contextual fear conditioning. This outcome is inconsistent with the saliency enhancement view of the context facilitation effect, but is exactly what is predicted by the conjunctive representation view.

Experiment 2

Experiment 2 was similar to Experiment 1 in that it was designed to provide evidence that rats construct conjunctive, not elemental, representations of the features of the context. However, the preexposure procedures differed from those used in Experiment 1. In that experiment, one set of rats was exposed to the context and another set was exposed to the features so that, during preexposure, no features of the conditioning context were experienced in combination. In this experiment, we constructed four contexts (A, B, C, and D; see Figure 3). Context C was the conditioning context, and Context D was composed of a different set of features. Contexts A and B contained all of the same features as Contexts C and D but in different combinations. Rats in the *context-same* condition were preexposed to Contexts C and D. Rats in the *context-shift* condition were preexposed to Contexts A and B. Rats in the control condition were

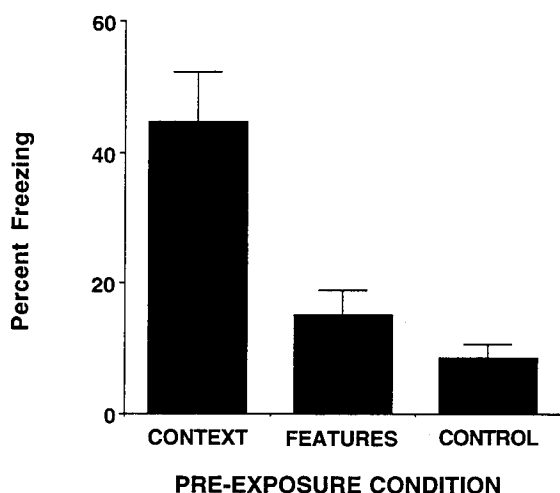


Figure 2. Mean percentage of freezing as a function of preexposure conditions used in Experiment 1. Bars represent standard errors of the mean.

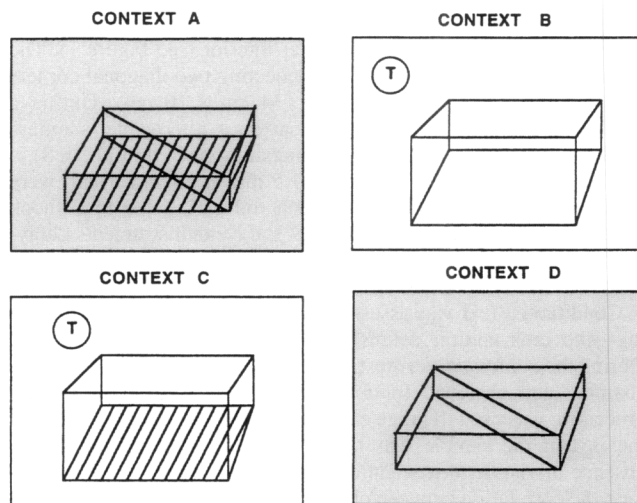


Figure 3. Illustration of the four contexts used in Experiment 2. Differences in shading represent differences in illumination of the ice chests. The circled T represents the presence of a tone that was continuously on.

preexposed to an opaque mouse cage that contained none of the features of the conditioning context.

Rats in the context-same and context-shift conditions had equal experience with the various features that composed the conditioning context. So, if rats learn only about features then it should not matter whether they were exposed to these features jointly or separately. However, if rats store conjunctive representations of the specific features, then the two groups should differ because only rats in the context-same condition were preexposed to the exact combination of features that made up the conditioning context.

The original strategy behind this experiment was to exploit the latent inhibition paradigm (Lubow, 1973). *Latent inhibition* refers to the fact that extensive preexposure to the cues of a conditioning experience can reduce conditioning to those cues. Kiernan and Westbrook (1993) have reported that, although limited exposure to the conditioning context can facilitate conditioning to that context, extensive exposure to the context can reduce conditioning. They also argued that this reduced conditioning (latent inhibition) resulted from rats having built up strong conjunctive-like representations of the context. This view predicts that latent inhibition should occur only if the rats are exposed to the same combination of features used to create the conditioning context and that exposure to the independent features should not produce latent inhibition. Although we intended to evaluate the effects of the different preexposure treatments on latent inhibition, our parameters failed to produce latent inhibition, and instead we obtained a facilitation effect of context preexposure. Nevertheless, our results illuminate how the context is represented because, as described below, rats exposed to the features of the context did not show the facilitation effect.

Method

Male rats 40 days old were randomly assigned to three conditions ($n_s = 8$). There were four preexposure contexts that differed along four dimensions: (a) chamber, either the large rectangular chamber or the small triangular chamber; (b) floor, either the rods for delivering shock or a Plexiglas floor; (c) lighting, the ice chest illuminated by either a 6-W clear light bulb or a 6-W red light bulb; and (d) sound, a 75-dB 3000 Hz tone that was either continuously present or absent.

As shown in Figure 3, Context A was composed of the small triangular Plexiglas chamber, the rod floor, and red light. Context B consisted of the large rectangular chamber, the Plexiglas floor, the tone, and clear light. Context C consisted of the large chamber, the rod floor, the tone, and clear light. Context D consisted of the small chamber, the Plexiglas floor, and red light.

Rats in the context-shift conditioning were preexposed to Contexts A and B, whereas rats in the context-same condition were preexposed to Contexts C and D. Note that exposing the two groups of rats to two contexts ensured that all rats had equal exposure to the features, while permitting only the rats in the context-same group to experience the conditioning context. Rats in the control condition were exposed to an opaque mouse cage, Context E, to equate for handling. Twice each day for 4 days, each rat was exposed to a context for 10 min. Daily exposures were separated by 1 hr. On Day 5, all rats were placed in the conditioning context, Context C, and 120 s later, they received a 0.4-mA, 2-s shock. Two subjects had to be eliminated because of experimental error. The next day, each rat was placed in the conditioning context, and freezing was scored for 5 min.

Results and Discussion

As shown in Figure 4, rats in the context-same condition displayed enhanced contextual fear conditioning in comparison with rats in the control condition. In contrast, rats in the context-shift condition did not differ from rats in the control condition. An analysis of variance (ANOVA) revealed differences between the groups, $F(2, 19) = 3.70, p < .05$. Post hoc tests indicated that rats in the context-same condition differed from the other groups ($p < .05$).

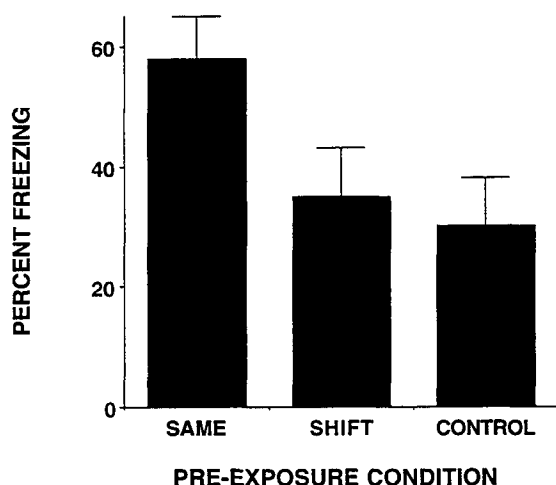


Figure 4. Mean percentage of freezing as a function of preexposure conditions used in Experiment 2. Bars represent standard errors of the mean.

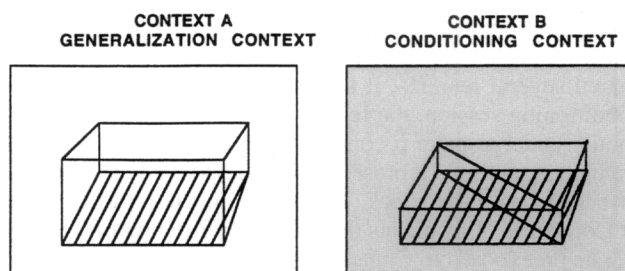


Figure 5. Illustration of the two contexts used in Experiment 3. Differences in shading represent differences in illumination.

Even though rats in the context-same and context-shift conditions had equal experience with the features of the conditioning context, only the rats in the context-same condition showed enhanced contextual fear conditioning. This outcome argues against the view that rats are learning only about the individual features of the context and instead supports the idea that they store a representation of the specific conjunction of stimuli that define a particular environment.

As noted, we expected that the lengthy preexposure to the training context would produce latent inhibition. Instead, it facilitated contextual fear conditioning, which we attribute to the strengthening of the conjunctive context representations. We are not sure why this experiment failed to produce latent inhibition (see also, Young & Fanselow, 1992). Although the rats in the context-same condition were exposed for a total of 40 min to each conditioning context, this might not have been enough exposure to produce latent inhibition to the context. Regardless of the failure to obtain a latent inhibition effect, however, the results are consistent with the idea that context is represented as the conjunction of its features.

Experiment 3

An important implication of the idea that context is represented as a conjunction of features is that such a representation permits *pattern completion*: A subset of the original features of an input pattern can activate the memory of the original pattern of input features (i.e., complete the original input pattern). Pattern completion is central to several computational and precomputational theories of how the hippocampus is involved in memory (e.g., McClelland et al., 1995; McNaughton & Morris, 1987; Squire, 1992; Tyler & DiScenna, 1986). As noted in the introduction, one hypothesis about why a conjunctive representation could support more fear conditioning than a salient-features representation is that a subset of the features can activate the entire neural network. However, if context is represented as a conjunction of features, then it should be possible to demonstrate the operation of the pattern completion process in another way.

To more directly assess whether intact rats exhibit pattern completion, we constructed two contexts, A and B, which shared several features (see Figure 5). Rats were preexposed to Context A and conditioned to Context B. Preexposure to

Context A should establish an integrated conjunctive representation of that context. Because Context A and Context B shared several features, it seemed possible that, during the conditioning session, the features common to both A and B should undergo pattern completion to the representation of Context A, and this representation would thus have become associated with the shock, in addition to the representation of Context B. This means that after conditioning to Context B, rats preexposed to Context A should have displayed more generalized fear to A than 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 either Context A or B. All rats were conditioned in Context B. Half of the rats in both preexposure conditions were then tested for contextual fear in Context B, and the other half were tested in Context A.

Method

Male rats 45 days old were randomly assigned to four conditions ($n_s = 7$). Context A consisted of the rectangular Plexiglas chamber placed on the stainless-steel rod floor inside the ice chest, which was illuminated by a clear 6-W bulb. The external door of the ice chest remained open, and the laboratory was illuminated with a 60-W frosted bulb. Context B consisted of the triangular Plexiglas chamber placed on the rod floor inside the ice chest, which was illuminated by a red 6-W bulb. When the rat was placed in the chamber, the door to the ice chest was closed and the room was dimly illuminated. Thus, these two contexts shared several features including room location and rod floor, as well as ambient noise produced by the ventilation fan. The control context (Context C) was the opaque mouse cage, which was placed in the central laboratory and had no features in common with Contexts A or B.

Approximately 24 hr before conditioning, rats were preexposed to either Context A for 4 min or to the control context. All rats were then conditioned to Context B. Each rat was placed into Context B, and 120 s later, the first of two shocks occurred. The second shock was delivered 120 s after the first shock. The next day, half the rats in each preexposure condition were tested for 5 min for fear conditioning in Context A (Conditions A-A and C-A), and the other half were tested for fear in Context B (Conditions A-B and C-B).

Results and Discussion

It is clear from Figure 6 that preexposure to Context A had no influence on freezing to the training Context B but dramatically influenced freezing in Context A. Rats preexposed to Context A displayed as much freezing in Context A as they did in Context B, and they displayed more freezing in Context A than did the rats in the control condition. Rats in the control condition displayed more freezing in Context B than in Context A. A 2×2 , between-subjects ANOVA revealed a main effect of preexposure, $F(1, 24) = 5.05$, $p < .03$; test context, $F(1, 24) = 5.79$, $p < .03$; and a significant Preexposure \times Test Context interaction, $F(1, 24) = 5.50$, $p < .03$. An analysis of the simple effects indicated that the test context was only significant for rats in the control condition, $F(1, 24) = 11.30$, $p < .003$, and that there were differences between the rats tested in Context A, $F(1, 24) = 10.60$, $p < .003$.

Preexposure to Context A clearly enhanced generalized fear to Context A. These results are consistent with the idea that the subset of elements shared by Context A and B resulted in pattern completion to the Context A representation, which was associated with shock. There is, however, an alternative, saliency-enhancement explanation of these results. Perhaps as a consequence of preexposure to Context A, the saliency of the features common to Context B was enhanced, and therefore those features were more strongly associated with shock. Thus, the enhanced generalized fear to Context A was not due to the network representing A being activated at the time of conditioning but was simply due to increased conditioning to the common features.

Experiments 4A and 4B

The conjunctive context and saliency enhancement interpretations differ on how they interpret the influence that preexposure to Context A has on the features common to Contexts A and B. The conjunctive view assumes that preexposure to Context A binds the common features into a network that also includes the unique features of A. The saliency interpretation assumes that preexposure enhances the saliency of only those features common to both Contexts A and B. There is a simple way to determine which view is correct: If the saliency enhancement view is correct then preexposure to Context B should produce as much generalized fear to Context A as preexposure to A. This follows because, according to the saliency view, preexposure to either Context A or B should enhance the salience of the common features. In contrast, the conjunctive view predicts that only preexposure to Context A should enhance generalized fear to A. This is because the common features can only enhance generalized fear to Context A if they have become bound with the unique features of A prior to conditioning.

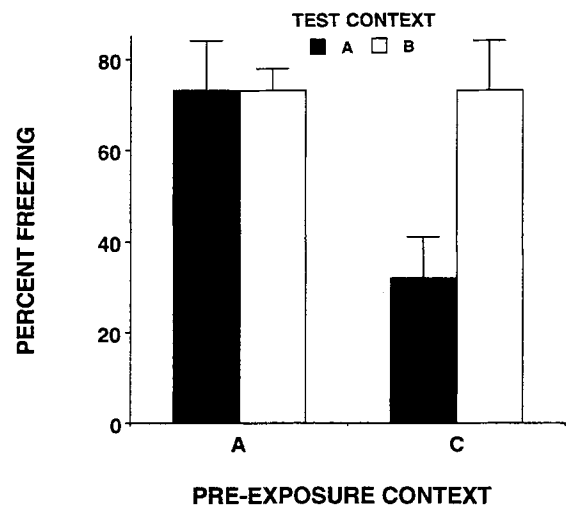


Figure 6. Mean percentage of freezing as a function of the preexposure contexts used in Experiment 3. All rats were conditioned in Context B. Half the rats were tested for generalized fear in Context A, and half were tested for specific contextual fear in Context B. Bars represent standard errors of the mean.

Experiment 4A was designed to compare the effects of preexposure to Context A or B on generalized fear conditioning to Context A after conditioning to Context B. To ensure that preexposure to Context A did not enhance conditioning to Context B, in Experiment 4B we compared the effects of preexposure to Context A or B on conditioned responding to Context B.

Method

Male rats 45 days old were preexposed for 4 min to Context A, Context B, or Context C, as described in Experiment 3. The next day, all subjects were conditioned to Context B. Approximately 24 hr later, rats in Experiment 4A were tested for freezing in Context A, and rats in Experiment 4B were tested for responding to Context B. Because there was a possibility that freezing in Context B was at the maximum level, rats in Experiment 4B were given a second 5-min test 24 hr after the first test. There were 13–14 subjects in each condition of Experiment 4A and 5–6 subjects in the three conditions of Experiment 4B.

Results and Discussion

As shown in Figure 7, there were differences, $F(2, 38) = 8.80$, $p < .007$, between the groups tested for generalized responding to Context A (Experiment 4A). Post hoc Newman-Keuls tests showed that rats preexposed to Context A displayed more freezing than rats in either of the other two conditions ($p < .01$), and that rats preexposed to Context B actually displayed less freezing than rats preexposed to Context C ($p < .05$). Figure 8 shows that there were no differences among the groups tested for conditioned fear responding in Context B on either the first or second test ($F < 1$).

The variation in generalized fear conditioning to Context A could have resulted from the various preexposure treatments differentially influencing the amount of fear conditioned to Context B (training context). The results of

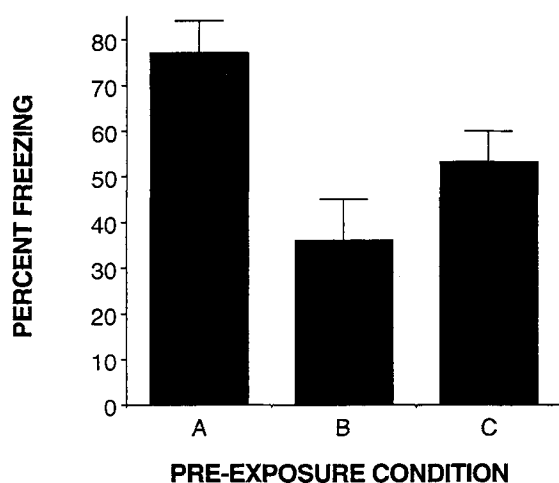


Figure 7. Mean percentage of freezing as a function of preexposure conditions used in Experiment 4A. All rats were conditioned in Context B and tested for generalized fear in Context A. Bars represent standard errors of the mean.

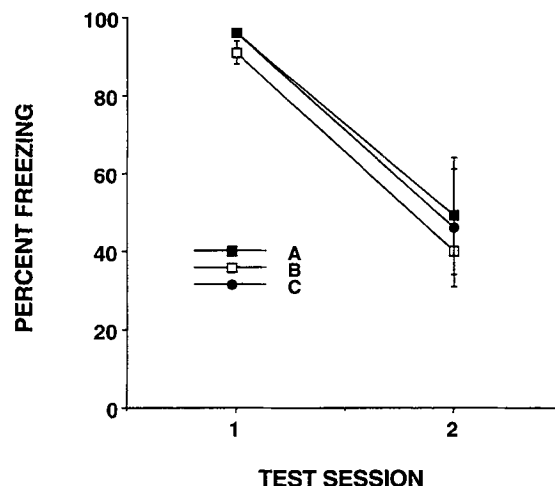


Figure 8. Mean percentage of freezing as a function of test session in Experiment 4B. All rats were conditioned and tested in Context B. They were preexposed to either Context A, B, or C. Bars represent standard errors of the mean.

Experiment 4B, however, indicated that the overall level of conditioned responding to Context B was the same regardless of whether the rats were preexposed to Context A, B, or C. Thus, the variation in generalized conditioned responding to Context A was not due to the effect of preexposure treatments on conditioning to Context B.

These data are inconsistent with the saliency enhancement interpretation of why preexposure to Context A enhances generalized conditioning to A. Such an interpretation would predict that preexposure to Context A or B should equally enhance generalized fear to A. This did not happen. In fact, preexposure to Context B *decreased* conditioning to Context A relative to the control condition, which supports the conjunctive view of why preexposure to Context A enhances generalized fear conditioning to A. Only when preexposure provided the opportunity for the common features to become bound in a representation that contained the unique features of Context A did preexposure enhance generalized conditioned responding to A.

That preexposure to Context B reduced generalized fear to Context A may be an artifact of rats in the control condition that were exposed to the Context C having displayed a high level of freezing. Note that the rats in Experiment 3 that received the same treatment displayed much less freezing than was observed in this experiment (Experiment 4A). Nevertheless, it should be noted that Kiernan and Westbrook (1993) also reported that preexposure to conditioning context can reduce generalized conditioning to other, similar contexts. This phenomenon is referred to as *pattern separation*, a process that reduces generalization to and interference from other similar experiences by separating different hippocampal representations from each other. Pattern separation has been shown to be a natural consequence of the use of sparse representations, and the idea that the hippocampus uses pattern separation to perform rapid learning while minimizing interference originated in a study by Marr (1971). Pattern separation can be

viewed as the complement of pattern completion, and it is possible to understand many aspects of hippocampal function in terms of the tradeoff between these two processes (O'Reilly & McClelland, 1994). Thus, it is also possible that preexposure to Context B in this experiment engaged hippocampal pattern separation, resulting in the observed reduction in generalization of the fear response in Context A.

Finally, we have assumed that generalized conditioning to Context A is enhanced because at the time of conditioning the neural network representing Context A, which is directly associated with shock, is activated by the features common to both contexts. Alternatively, one could argue that generalized conditioning occurs because, during the test, the shared features activate the Context B network and that fear associated with the B network provides the fear shown to A. The results of both Experiments 3 and 4 appear to rule out this interpretation because, if it were true, all rats should have displayed the same amount of generalized fear to Context A because conditioning to Context B was the same for all groups.

Experiment 5

We have proposed that the enhanced generalization to Context A that results from preexposure to it is a product of associating the conjunctive representation of its unique features with shock by the pattern completion process. Alternatively, one could argue that the enhanced generalized fear to Context A was simply a performance effect. By this account, control rats that were not preexposed to A displayed less generalized fear because when they encountered the Context A, its unique features of A were novel and the reaction to novelty interfered with the retrieval of the fear response by the features shared by Contexts A and B. This would be a form of what Pavlov called *external inhibition*, the disruption of conditioned responding by a novel stimulus. Rats preexposed to Context A did not experience external inhibition, because its unique features were familiar. Therefore, the common features were able to fully activate the fear response.

The purpose of Experiment 5 was to provide data relevant to the pattern completion (learning) versus external inhibition (performance) accounts of the enhanced generalization of fear observed in Experiments 3 and 4. The essence of the external inhibition account is that the novel features of Context A interfered with the retrieval of fear by the features common to Contexts A and B. Thus, we designed the experiment to provide a preexposure treatment that, in principle, would reduce the novelty of the unique features that differentiate Context A from Context B. As in the previous experiment, rats in one condition were preexposed to Context A, and another set of rats were preexposed to Context C. However rats in the new condition were preexposed to *all the features* that made up Context A, but they were experienced separately (similar to Experiment 1). All rats were then conditioned to Context B and tested for generalized fear to Context A. If the novelty of Context A's unique features interfered with the expression of generalized fear displayed by rats preexposed to Context C, then the

external inhibition hypothesis would predict that rats preexposed to all features of Context A should also display enhanced generalization to A. However, the pattern completion interpretation predicts that preexposure to the independent features should not enhance generalization to Context A, because these features would not be bound together in a conjunctive representation.

In addition to evaluating the features-based interpretation of enhanced generalization, to extend the generality of the phenomenon of enhanced generalization, we used both male and female subjects that were older than those used in previous studies (52–55 days old). Maren, De Oca, and Fanselow (1994) have reported that male rats display more contextual fear than female rats, and we wanted to be sure that sex did not interact with the effect of preexposure on generalized fear.

Method

Four male and 4 female rats 52–55 days old were assigned to each of the three conditions. All rats were conditioned to Context B and tested for generalized fear in Context A. They differed in their preexposure treatments. Rats in the context condition were exposed to Context A, which consisted of the rectangular Plexiglas chamber placed on the rod floor inside the ice chest, which was illuminated by a clear 6-W bulb. The external door of the ice chest remained open. Rats in the features condition were exposed to the separable features of Context A, and rats in the control condition were exposed to Context C (the opaque mouse cage).

Rats in the features group were treated as follows. First, they were exposed to the shock rods. This was accomplished by placing the rod floor in the central laboratory room and placing the rats in a transparent mouse cage atop the rod floor. Forty minutes later, they were exposed to the rectangular Plexiglas chamber, which was placed on a smooth Plexiglas floor in the central laboratory room. Finally, 2 hr later, they were exposed to the ice chest in the room where conditioning took place. This was done by placing the rat in a transparent mouse cage that rested on a smooth Plexiglas floor inside the ice chest. The room lighting and internal lighting of the ice chest were identical to that of Context A. The duration of exposure to each feature was 4 min. To equate for handling, rats exposed to Context A were also given 3 exposure treatments. They were given two 4-min exposures to the opaque mouse cage and were then exposed to Context A for 4 min. Subjects in the Context C condition were exposed three times to the opaque mouse cage.

Results

As shown in Figure 9, rats preexposed to Context A displayed enhanced generalized fear, but rats preexposed to the features that made up Context A did not. A Sex \times Preexposure treatment ANOVA revealed only a main effect of sex, $F(2, 18) = 7.70$, $p < .01$, and preexposure treatment, $F(2, 18) = 22.70$, $p < .001$. However, the Sex \times Preexposure treatment interaction was not significant, $F(2, 18) = 2.60$, $p = .10$. Post hoc Newman-Keuls comparisons revealed that rats preexposed to Context A differed from rats in the other conditions ($p < .01$). No other differences were statistically significant.

We replicated Maren et al.'s (1994) finding that male rats display more contextual fear than females. Preexposure to

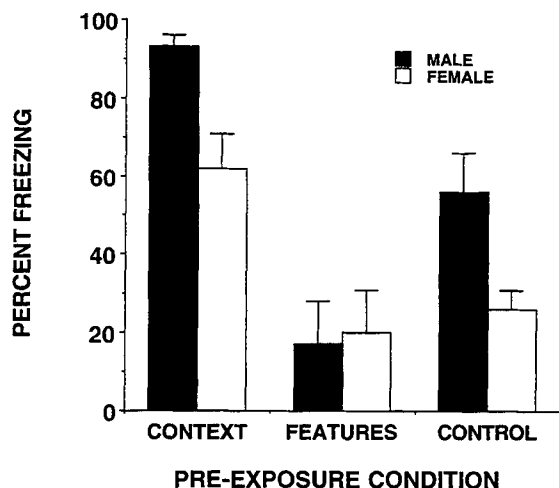


Figure 9. Mean percentage of freezing as a function of preexposure conditions used in Experiment 5. All rats were conditioned in Context B and tested for generalized fear in Context A. Bars represent standard errors of the mean.

Context A, however, enhanced generalized fear to Context A in both male and female rats. Thus, sex does not interact with the effect of preexposure on generalized fear. Maren et al. (1994) also reported a sex difference in long-term potentiation induced at perforant path synapses in the dentate gyrus of the hippocampus and suggested that this difference may provide a mechanism for the sex difference in contextual fear conditioning.

According to the external inhibition account of generalized contextual fear, preexposure to the independent features of Context A should enhance generalized fear to Context A by rendering those features familiar and less distracting. Thus, these results offer no support for the external inhibition account, because preexposure to the features actually reduced generalized fear to Context A. These results, however, are consistent with the pattern completion interpretation because this account predicts that only preexposure to Context A should enhance generalized fear to Context A.

There is, however, an alternative, conjunctive representation-based account of these data. One could still argue that the enhanced generalization to Context A resulting from preexposure to Context A was a performance effect. The argument would be that, although rats in the features condition were familiar with all the features of Context A, the conjunction of these features was novel, and this novel conjunction interfered with the retrieval of the fear response by the features common to A. This account is not implausible and is compatible with the conjunctive representation view of context. Nevertheless, if the conjunctive representation of Context A is so easily discriminated from other contexts that contained some of its features, including the conditioning context (B), then one would have to wonder why there was so much generalization to Context A after conditioning to Context B. Our answer to this question is that, because of the pattern completion process, the network containing the unique features of Context A was associated with shock.

General Discussion

We evaluated two interpretations of why preexposure to a conditioning context can facilitate subsequent conditioning to that context. The conjunctive representation account assumes that contextual fear conditioning is mediated in large part by a system in which the independent features of the context are bound together into a unitary representation. According to this view, preexposure facilitates conditioning because it allows this representation to be constructed prior to conditioning. Consequently, even though the rats might be attending to a subset of the features that make up the context, all the features bound into the network become associated with shock because the entire network is active at the time of conditioning. In contrast, the saliency enhancement account assumes that the independent features of the context are associated with shock, and that preexposure to the context facilitates conditioning by enhancing the saliency of each feature, thereby increasing their ability to associate with context.

The saliency enhancement interpretation predicts that preexposure to the independent features of a context should influence contextual fear conditioning as much as preexposure to the context as a whole. The results of Experiments 1 and 2, however, indicate that preexposure to the features did not facilitate contextual fear conditioning. Only preexposure to the conjunction of features that defined the conditioning context resulted in facilitation. These results strongly support the conjunctive representation view.

Three other experiments found that preexposure to a context (A) that shared features with the conditioning context (B) increased generalized fear to Context A. This result could not be attributed to preexposure enhancing the saliency of the common features because preexposure to Context B did not enhance generalized fear to Context A. In addition, this result could not be attributed to the novelty of the unique features that define Context A interfering with the activation of the conditioned fear response. These results also strongly support the conjunctive account, according to which enhanced generalized fear to A is seen as an instance of pattern completion that can be produced by a conjunctive representation. As a consequence of preexposure to Context A, its unique features were bound with those features shared with Context B. Consequently, during conditioning, the representation of Context A was activated by the subset of features shared with Context B, and this representation was associated with shock.

As noted in the introduction, it has often been argued that the construction of a conjunctive representation of context requires the participation of the hippocampal formation (Nadel & Willner, 1980; Nadel et al., 1985). Moreover, there is evidence that contextual fear conditioning is impaired by damage to the hippocampal formation (e.g., Frankland, Cestari, Filipkowski, McDonald, & Silva, 1998; Kim & Fanselow, 1992; Maren et al., 1997; Phillips & LeDoux, 1994), and this impairment has been attributed to the loss of the conjunctive representation of context (Fanselow & Rudy, 1998; Maren et al., 1997; Rudy & Sutherland, 1992, 1994, 1995; Young et al., 1994). What has

been lacking is strong evidence that normal rats actually construct a conjunctive representation of context. Thus, the primary importance of the present experiments is that they provide compelling evidence that a conjunctive representation makes a significant contribution to contextual fear in the normal rat.

We also noted in the introduction that it is somewhat surprising that damage to the hippocampal formation impairs contextual fear conditioning because independent features of the context should also be capable of associating with shock. It is thus interesting that there have been recent reports that damage to the hippocampal formation *prior* to contextual fear conditioning (i.e., an anterograde lesion) has either no effect or a weak effect on contextual fear conditioning (Frankland et al., 1998; Maren et al., 1997). In contrast, damage to the hippocampal formation after conditioning (i.e., a retrograde lesion) severely impairs contextual fear conditioning in rats and mice (Anagnostaras et al., 1999; Frankland et al., 1998; Kim & Fanselow, 1992; Maren et al., 1997). We think that Maren et al. (1997) have provided a reasonable account of the variable anterograde effects versus the stable and strong retrograde effects of hippocampal formation damage: The normal rat naturally forms a neural representation of the conjunction of features that define the context. Consequently, postconditioning damage to the hippocampal formation will severely impair contextual fear because conditioning occurs primarily to this conjunctive representation in the hippocampus. In the absence of the hippocampal formation-dependent conjunction representation, rats can still condition to one or more features. Thus, depending on as-yet-uncharacterized parameters, contextual fear conditioning in rats with damage to the hippocampal formation will not necessarily be severely impaired. Maren et al., in fact suggested that during the postlesion interval, rats might actually learn a compensating strategy for using the independent features.

Because contextual fear conditioning can be mediated by conditioning to either the representations of the individual elements or to the representation of their conjunction, it is difficult to know how to interpret a null effect seen after damage to the hippocampus. Thus, if one believes that the hippocampus contributes to contextual fear conditioning by rapidly constructing a conjunctive representation of the context, then we suggest that the most appropriate paradigms to study are those associated with context preexposure (as was the focus of the experiments reported here). For example, we would predict that damage to the hippocampus prior to contextual preexposure would eliminate the preexposure facilitation effects seen in normal subjects. To our knowledge, such a study has not yet been conducted. A retrograde hippocampal lesion study by Young et al. (1994) found no impairment after preexposure, but the delay between preexposure and conditioning was intentionally set to be long enough (28 days) to allow the conjunctive context representations to be incorporated into cortical representations (e.g., by consolidation from off-line rehearsal; McClelland et al., 1995; Squire, 1992; Squire, Cohen, & Nadel, 1984). We would predict that damage to the hippocampus only 24 hr after preexposure would eliminate the facilitation

effect. A similar argument can be made regarding the generalized fear effects we reported here. If our pattern completion interpretation of why preexposure to Context A enhances generalization to A is correct, then damage to the hippocampus should reduce this effect. There are no data currently available to evaluate this hypothesis.

Relationship Between Contextual Fear and Other Learning Tasks That Depend on the Hippocampus

Our interpretation of the role of the hippocampus in contextual fear is quite general, and can easily be applied to other learning that is impaired by damage to the hippocampus. We think that the role of the hippocampus is to allow animals to rapidly and automatically store representations of stimulus conjunctions, simply as a function of the subject exploring and attending to its environment. We refer to this as *rapid incidental conjunctive learning* (O'Reilly & Rudy, 1999). Recently, there have been a number of studies in a variety of other paradigms that support this general view. They include studies of the habituation of exploratory behavior (Save, Poucet, Foreman, & Buhot, 1992), habituation of the orienting response (Honey, Watt, & Good, 1998), and the context-specificity effect observed in Pavlovian conditioning (Good & Bannerman, 1997; Honey & Good, 1993).

These studies all provide evidence that animals automatically store representations of stimulus conjunctions even though there is nothing about these tasks that requires such learning. The incidental conjunctive learning was revealed by transfer tests that occurred after training, in which the relationship among the features was varied. These studies also show that this learning depends on the hippocampus. Three examples are discussed below.

In a study of exploratory behavior, Save et al. (1992) repeatedly exposed control rats and rats with damage to the dorsal hippocampus to a set of objects that were arranged on a circular platform in a fixed configuration relative to a large, distinct visual cue. After the exploratory behavior of both sets of rats habituated, the same objects were rearranged into a different configuration. This rearrangement reinstated exploratory behavior in the control rats but not in the rats with hippocampal damage. In a third phase of the study, a new object was introduced into the arrangement, which reinstated exploratory behavior in both sets of rats. This pattern of results suggests that both control rats and rats with hippocampal damage encode representations of the individual objects and can discriminate between familiar and novel objects. However, only the control rats encoded the conjunctions necessary to represent the spatial arrangement of the objects. Note that this was not a requirement of the task; all subjects could have habituated simply because they stored representations of the individual objects.

A more recent article by Honey et al. (1998) made a similar point. In their study, the rats' orienting response habituated to different sequences of auditory and visual stimuli. A tone was followed by the presentation of a constant light source, whereas a train of clicks was followed by a flashing light source. The orienting response to the

constant and flashing light habituated in both control rats and rats with hippocampal damage. However, during a transfer test, in which the auditory and visual combinations were reversed (the clicks preceded the constant light and the tone signaled the flashing light) the orienting response to the light was reinstated in the control rats but not in the rats with damage to the hippocampal formation. Thus, whereas Save et al. (1992) reinstated the habituated response by rearranging the spatial locations of the objects, Honey et al. (1998) reinstated the habituated response simply by altering the stimulus sequence. In both cases, the acquisition of incidental conjunctive appeared to require the hippocampus.

There is also evidence from Pavlovian conditioning studies that normal rats learn stimulus conjunctions that are not required by the task. This phenomenon, termed the *context specificity effect*, is observed in intact rats (Hall & Honey, 1990; Honey, Willis, & Hall, 1990). If rats are conditioned to Cue A in Context 1 and Cue B in Context 2, they will display more conditioning to Cue A in Context 1 than in Context 2 and more conditioning to Cue B in Context 2 than in Context 1. Context specificity cannot occur unless the rat stores a conjunctive representation of the cue and the context features, because all the elemental features of the experiment should be equally associated with the US (Rudy & Sutherland, 1995). Thus, if responding were controlled only by the associative strengths of the independent elements, there should be no context specificity of conditioning. Although intact rats display the context specificity effect, Honey and Good (1993; see also Good & Bannerman, 1997) reported that rats with damage to the hippocampal formation do not. They respond equally to the cues, regardless of context.

The studies implicating the hippocampus as central to the automatic storage of stimulus conjunctions can be contrasted with other studies that have investigated Sutherland and Rudy's (1989) theory that the hippocampus represents stimulus configurations (conjunctions). Sutherland and Rudy argued that if this is the case, then subjects with damage to the hippocampus should not be able to solve nonlinear discrimination learning problems that depend on the representation of stimulus conjunctions. The negative patterning problem is a good example of such problems. The subject is reinforced (+) in the presence of individual features, A and B, and nonreinforced (−) in the presence of the AB compound (A+, B+, AB−). Note that correct performance on this problem can only occur if the subject constructs a conjunctive representation of the AB compound. On the basis of existing literature, however, one has to reject the idea that the hippocampus stores representations of stimulus conjunctions because there are a number of compelling reports of subjects with damage to the hippocampus solving nonlinear discriminations (for a review, see Rudy & Sutherland, 1995; Alvarado & Rudy, 1995; Cho & Kesner, 1995; Davidson, McKernan, & Jarrard, 1993; Gallagher & Holland, 1992; McDonald et al., 1997; Whishaw & Tomie, 1991).

To reconcile the nonlinear discrimination data with the rapid incidental conjunctive learning in the studies just described, one must appreciate that nonlinear discrimination

problems can be solved only if the subject constructs a representation of the conjunction of stimulus features. Thus, the subject is forced to construct the conjunctions by the demands of the task, and such learning requires many training trials. We suggest that under these conditions, the neocortex is able to learn conjunctive representations without a hippocampus (O'Reilly & Rudy, 1999). In contrast, we consider the rapid learning of conjunctions unforced by task demands (incidental learning) to be a unique function of the hippocampus.

We have integrated the above ideas into an explicit, biologically based neural network model of the neocortex and the hippocampus that implements a basic set of computational principles to capture what we think are the fundamental distinctions between cortical and hippocampal learning (O'Reilly & Rudy, 1999). Our model accounts for the data we have presented in this article, the findings mentioned above implicating the involvement of the hippocampus in the rapid incidental learning of stimulus conjunctions, and the complex pattern of data obtained in nonlinear discrimination studies.

Relationship to Other Accounts of the Role of the Hippocampus

We note that our view has much in common with the ideas O'Keefe and Nadel (1978) put forth in distinguishing between *locale* learning, which depends on the hippocampus, and *taxon* learning, which does not. Our framework links contextual fear conditioning with other evidence that the hippocampus automatically stores conjunctions and contrasts this process with conjunctive learning that is forced by the task. Although most of the literature generated by the O'Keefe and Nadel (1978) theory has focused on the idea that the hippocampus provides the basis for a spatial map (which can be viewed as a special instance of a conjunctive representation), their theory also distinguished between the two systems on other dimensions. Two of these that relate to our view are (a) *learning rate*, in which the locale system is viewed as rapidly storing new information, whereas the taxon system learns and unlearns by slow increments; and (b) *motivation*, in which 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 engaged in the service of problem solving or achieving goals and is therefore sensitive to the reinforcement contingencies associated with behavior.

It should also be noted that the idea that the hippocampal formation is best conceived of as a rapid automatic storage device has appeared early in the history of theorizing about the hippocampus (e.g., Marr, 1971). It is also present in other, more contemporary views (e.g., McNaughton & Morris, 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, as 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.

We also reiterate that the ideas that generated our experiments on context preexposure allow the study of contextual learning to overlap at the mechanistic level (in terms of pattern completion) with Squire's (1992) view of declarative memory, which is thought to depend on the hippocampus. In humans, declarative memory is said to support conscious recollection of past experience. Squire has suggested that this property may be linked to the pattern-completion properties of the hippocampus. He noted that

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)

A similar idea is at the heart of Tyler and DiScenna's (1986) indexing theory of hippocampal involvement in memory.

Relationship to Perceptual Learning Models and Sensory Preconditioning

The context preexposure paradigm, which we think is the most informative for understanding the unique contributions of the hippocampus to contextual fear conditioning, may also be related to perceptual learning and sensory preconditioning paradigms studied in classical conditioning experiments (Brogden, 1939; Gibson & Walk, 1956; Hall, 1980; McLaren, Kaye, & Mackintosh, 1989). In these paradigms, subjects are exposed to stimuli prior to the use of these stimuli as CSs in conditioning experiments.

Perceptual learning refers to the fact that previous exposure to stimuli can facilitate the rate at which animals can learn to discriminate between them when they are subsequently differentially associated with reward. McLaren et al. (1989) developed a model that explains perceptual learning by assuming that preexposure results in the formation of associative links among the stimulus features. This idea is similar to the view that stimuli that co-occur are stored as stimulus conjunctions. McLaren et al. did not make any explicit claims about the role of the hippocampus in perceptual learning; however, our framework suggests that the hippocampus could also play an important role in this phenomenon. We are not aware of experiments that have tested this idea in the perceptual learning paradigm.

It is also possible that the McLaren et al. model could provide some insight into the contextual preexposure paradigm examined in the present study. In fact, Kiernan and Westbrook (1993) explicitly offered McLaren et al.'s (1989) model as a way to account for their finding that context preexposure facilitates contextual fear conditioning. The primary difference between the McLaren et al. model and our own view is that they postulate that stimulus associations are formed directly among the stimuli themselves,

whereas our model holds that separate, conjunctive hippocampal representations are used to bind together stimulus representations. Many behavioral tests would fail to distinguish between these two different views. Nevertheless, the fact that hippocampal lesions appear to specifically impair the conjunctive associations among stimuli, but not the representations of the stimuli themselves (e.g., Honey et al., 1998; Save et al., 1992), provides some support for the idea that these associations are often mediated by the hippocampus and are not directly formed among the stimulus representations themselves. However, we think that with extensive exposure, or if the demands of the task require that stimulus conjunctions be represented, they may be learned even without a contribution of the hippocampus.

In a sensory preconditioning task (Brogden, 1939), the subject is exposed to two stimuli in compound (e.g., AB) and is then conditioned to one (e.g., B-US). Sensory preconditioning is said to occur when the other member of the compound, A, elicits a conditioned response. When proper control procedures are included, one can safely conclude that sensory preconditioning occurs because the subject has associated the two stimuli during the preconditioning phase of training (Rizely & Rescorla, 1972). Such learning is sometimes referred to as within-compound learning (Rescorla & Cunningham, 1978).

Three points should be made about sensory preconditioning in the context of the present study. First, the enhanced generalized contextual fear that we report to Context A after preexposure to Context A and conditioning to Context B is conceptually similar to sensory preconditioning. According to our analysis, this generalization occurs because the features unique to Context A are stored in conjunction with the features common to Contexts A and B. These common features are present at the time of conditioning and trigger pattern completion such that Context A's unique features become conditioned, resulting in enhanced generalized fear to Context A. Second, the learning that occurs in sensory preconditioning as a product of preexposure to AB is *not required* by any demands of the task but is an automatic product of the subject noticing the AB event. Finally, there is some evidence that sensory preconditioning might also depend on the hippocampus (Port & Patterson, 1984), which supports our argument that the hippocampus is important for storing stimulus conjunctions when they are not demanded by the demands of the task.

Conclusion

In summary, the experiments presented in this article provide strong support for the idea that normal rats represent a conditioning context as a conjunction of features. This conclusion was arrived at by demonstrating that preexposure to the conditioning context facilitated contextual fear conditioning, whereas exposure to the independent features did not. We also examined the implications of the conjunctive view of context for generalized fear, in which a conjunctive representation permits pattern completion to a preexposed context (A), as a function of features shared with the conditioning context (B). This result was observed in several

experiments. Several researchers have proposed that damage to the hippocampus impairs contextual fear conditioning because rats with impaired hippocampal-formation processing cannot form conjunctive representations. These experiments provide support for this interpretation. Finally, our theoretical analysis suggests that the mechanism of pattern completion provides a critical link for understanding the role of the hippocampus in contextual fear conditioning, other incidental conjunctive learning paradigms, and human declarative memory.

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Received October 28, 1998

Revision received March 18, 1999

Accepted June 2, 1999 ■