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Research report

Within-event learning in rats with lesions of the basolateral amygdala

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HIGHLIGHTS

- We examine BLA- and sham-lesioned rats' ability to form sensory–sensory associations.
- BLA-lesioned rats can acquire sensory preconditioning.
- BLA-lesioned rats are impaired at taste-potentiated odor aversion.
- BLA needed for learning sensory properties of motivationally significant stimuli.

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ABSTRACT

Rats with neurotoxic lesions of the basolateral amygdala were trained in procedures designed to assess the formation of within-event, taste–odor associations. In Experiments 1 and 2 the animals were given initial exposure to a taste–odor compound; the value of the taste was then modified, and the consequent change in responding to the odor was taken to indicate that an odor–taste association had been formed. In Experiment 1 the value of the taste (saline) was enhanced by means of salt-depletion procedure; in Experiment 2 the taste was devalued by aversive conditioning. In neither procedure did lesioned animals differ from sham-operated controls. Experiment 3 confirmed, however, that taste-potentiation of odor aversion learning (an effect thought to depend on the formation of a taste–odor association) is abolished by the lesion. Implications for the view that the amygdala is necessary for sensory–sensory associations between events in different modalities are considered.

1. Introduction

It is widely accepted that the amygdala complex is involved in learning about events of emotional or motivational significance. Much of the evidence comes from work with aversive events (e.g., [1–3]) but effects have also been obtained with appetitive reinforcers (e.g., [4,5]). In their analysis of these latter effects, Blundell et al. [6] demonstrated that lesions of the basolateral amygdala (BLA) had no effect on a rat's ability to acquire a Pavlovian conditioned response but that in instrumental learning the normal sensitivity to devaluation of the reinforcer was not obtained. Specifically, BLA-lesioned rats trained to make different responses for different reinforcers did not a show a selective reduction in responding when one of the reinforcers was devalued (e.g., by feeding the animal to satiety with that reinforcer). It was suggested in explanation, that the BLA is necessary for animals to form a representation of the reinforcer that integrates its sensory and motivational properties (see also Ref. [7]).

According to this interpretation, the deficit shown by rats with BLA lesions lies in their inability to learn normally about the sensory aspects of motivational events. The effect appears to be specific to the combination of motivational and sensory properties as other research has shown that their ability to form associations between two sensory aspects of a compound stimulus is unaffected. Thus, Blundell et al. [6] gave lesioned rats exposure to a compound of two tastes (e.g., salt and sucrose). One of these tastes was then devalued by pairing it with a nausea-inducing injection of lithium chloride (LiCl). In a subsequent test, the rats showed an aversion to the other taste; that is, a standard sensory preconditioning effect was obtained. Learning about the properties of the taste compound in the first stage, when the motivationally significance of the stimuli was not relevant, proceeded normally. (It is true that the rats were water-deprived during this experiment and that the flavors were presented as solutions, but the motivational significance of the stimuli was not relevant to the test which assessed only the association between the two tastes.)

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Dwyer and Killcross [8] confirmed this result, and then went on to look at a parallel procedure with hungry subjects. They gave rats exposure to a motivationally significant taste (e.g., sucrose) in a particular place (one arm of a Y-maze). They then devalued that arm by associating it with the effects of an injection of LiCl. When given a place-preference test, rats with lesions of the BLA showed a normal tendency to avoid that arm, demonstrating that they had learned about the motivational significance of that place. But, in contrast to control subjects, they showed no evidence of having acquired an aversion to the sucrose that had experienced there. Dwyer and Killcross concluded that, for rats with BLA lesions, the place cues were able to retrieve only a general motivational representation, so that experience of an aversion in that place would be unable to generate an aversion to the specific taste of sucrose [8].

This account of the effects of BLA lesions – that they impair the ability to learn about the sensory aspects of a motivationally significant event, but that sensory–sensory associations between neutral stimuli are not affected – is challenged by the results of studies of the phenomenon of taste-potentiated odor-aversion learning (TPOA). Rats given exposure to a taste shortly before a state of nausea is induced will readily develop an aversion to the taste; it is assumed that an association is formed between the taste as the conditioned stimulus (CS) and nausea as the unconditioned stimulus (US). Aversion learning with an odor as the CS, by contrast, proceeds only slowly. If, however, a taste is presented in compound with the odor, the aversion acquired by the odor is found to be stronger (e.g., [9]; see Ref. [10], for a review); that is, the presence of the taste potentiates conditioning to the odor. One interpretation of this effect is that it depends on a process of within-event learning [11]. The suggestion is that experience of the compound CS during conditioning allows the rat to form an odor–taste association. The taste also forms a strong association with the US, whereas the odor does not. The odor will be able to elicit a conditioned response (CR), however, not because of its own association with the US, but by way of the associative chain: odor–taste-US. Evidence in favor of this interpretation comes from the observation that extinction of the taste prior to the test with the odor (a procedure that will break the last link in the chain), reduces the ability of the odor to evoke the CR [12]. Thus, TPOA appears to rely on sensory–sensory learning, between neutral events.

If the BLA is specifically involved in learning about the sensory properties of motivationally significant events, there is no reason to expect an effect of BLA lesions on the sensory–sensory association taken to be responsible for TPOA. It has been reliably demonstrated, however, that procedures that disrupt the normal functioning of the BLA attenuate or eliminate TPOA. This result was first demonstrated in studies using electrolytic lesions [13] but has since been obtained with neurotoxic lesioning techniques [14,15], and with infusions into the BLA of the GABA receptor agonist muscimol [16] of the NMDA antagonist APV [17,18], of lidocaine [19] and of the noradrenalin antagonist propanolol [20]. Hatfield and Gallagher [17] further reported that the TPOA shown by normal animals in their training preparation is sensitive to the effects of extinguishing the taste, confirming the interpretation that the effect depends on the formation of the within-event, odor–taste association. In contrast to the results obtained with the sensory-preconditioning procedure then, these experiments appear to demonstrate a role for the BLA in the formation of sensory–sensory associations between motivationally neutral cues.

The TPOA procedure involves a compound cue with elements drawn from different modalities (i.e., a taste and an odor), and Hatfield and Gallagher [17] offered the interpretation that a normally functioning BLA is needed for the formation of associations between such cues. This interpretation can accommodate the results described so far. According to this line of reasoning, the failure of lesioned animals to a show a reinforcer devaluation effect is taken to be a specific instance of their inability to form a cross-modal association, in this case between the sensory and motivational properties of the reinforcer. Sensory preconditioning proceeded normally in the experiments cited earlier [6] because the critical stimuli were drawn from the same modality (both were tastes). The obvious implication of this analysis is that sensory preconditioning would be disrupted by BLA lesions if the relevant stimuli were taken from different modalities (e.g., if a taste and an odor were used, as in the TPOA procedure). The first two experiments to be reported here test this prediction; the final experiment looks again at TPOA using our stimuli and procedures.

Experiment 1 employed a procedure [21] that makes use of an experimentally induced salt need to demonstrate the formation of within-event taste–odor associations. In the version of this procedure developed in our laboratory, rats are allowed to consume a saline solution to which an odorant (iso-amyl acetate, AA) had been added. At the concentration used in this procedure, AA has been demonstrated to function strictly as an odor without taste properties [22]. The rats are then injected with an agent that produces sodium depletion and thus renders saline particularly valued. When given a choice between plain water and water to which AA had been added, normal rats show a marked preference for the latter. This outcome depends on the rats having experienced saline and AA together in the first phase; control subjects given exposure to saline and AA on separate trials during this phase show no preference for the odor of AA on test.

We investigated the effects of neurotoxic lesions of the BLA on performance on this task. There were four groups of subjects – BLA-lesioned and sham-lesioned subjects given preexposure to the taste–odor compound (Group Lesion-Comp and Sham-Comp), and lesioned and sham-lesioned subjects given separate exposure to the elements of the compound (Groups Lesion-Ele and Sham-Ele). We anticipated that animals in Group Sham-Comp would show a preference for AA on the test whereas those in Group Sham-Ele would not. If an intact BLA is necessary for the formation of a within-event, odor–taste, association, then neither of the lesioned groups would be expected to show such a preference.

Experiment 2 utilized an aversive conditioning paradigm to examine the effect of BLA lesions on the formation of taste–odor associations, using a procedure that has been widely applied in demonstrations of sensory preconditioning in flavor aversion learning [11]. This experiment employed a within-subject design. All rats were initially exposed to two compound stimuli, AX and BY, where A and B were different tastes and X and Y different odors. Again, there is good evidence that these stimuli function as odors at the concentrations used here [23]. They then received aversion conditioning with LiCl as the US and taste A as the CS; taste B was presented nonreinforced in this stage. The test assessed the extent to which odors X and Y controlled an aversion. If preexposure establishes within-event associations then it can be expected that establishing an aversion to X's associate would result in the animals showing an aversion to this odor on the test. Since Y's associate B does not undergo conditioning, no aversion to Y is to be expected. The question of central interest was whether lesions of the BLA would eliminate the X/Y difference.

Experiment 3 was a replication of the basic taste-potentiation effect, using a within-subject design. This experiment employed two odors, almond and vanilla. All animals receive two conditioning trials, one with each odor. On one of these trials an odor was presented alone; on the other trial, the other odor was presented in compound with a taste (sucrose). Separate tests assessed the aversion controlled by each odor. A stronger aversion to that trained in compound with sucrose than to that trained alone would indicate potentiation by taste. The question of interest was whether this effect would be found in rats with BLA lesions.