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5 February 1979; revised 2 April 1979

ACTH and Vasopressin Treatments Immediately After a Defeat Increase Future Submissiveness in Male Mice

Abstract. *Male mice were given a single injection of either adrenocorticotropic hormone (ACTH) or lysine vasopressin immediately after a defeat in an encounter with an aggressive male mouse. The defeated mice were tested for submissiveness at either 24 hours, 48 hours, or 7 days after the initial encounter. Both hormone treatments increased future submissiveness, although the time courses of the effects were different: The effects of ACTH disappeared after 48 hours, whereas those of vasopressin persisted for 7 days. These results suggest that changes in peptide hormone levels following naturally stressful experiences can affect the memory of those experiences, as expressed in future adaptive responses.*

Recent evidence has suggested that the hormonal responses to initial experiences may be important in the mediation of the effects of those experiences on future behavioral reactions, perhaps through effects on memory processes (*1*-*4*). The majority of this evidence comes from studies of the effects of the pituitary peptides adrenocorticotropic hormone (ACTH) and vasopressin on avoidance responding in rats and mice, where posttraining treatments with these hormones lead to enhanced retention of the avoidance response (*1*, *3*, *5*, *6*). We report here the results of two experiments showing that these pituitary peptides may play a similar role in social situations as well; increasing ACTH and vasopressin levels immediately after an initial defeat increases an animal's submissiveness in future encounters.

The experiments reported here examine the interaction between prior experiences of defeat and experimentally altered hormone levels. We conducted two initial studies: the first to show that prior experiences of defeat do increase future submissiveness, and the second to show that the hormone treatment schedule used here does not affect submissiveness independently of the prior experience of defeat (*7*). In this way, we could be certain that the design of the two experiments described here does permit evaluation of the interaction of prior experiences with modified hormone levels.

In the first experiment on the interaction of prior defeat and hormone treatment, we examined the effects of postdefeat treatments with ACTH on future submissiveness. Fifty-nine male CD-1 mice, 7 weeks old and kept isolated from other mice for 1 week, experienced an initial defeat in an encounter with an aggressive opponent. The opponents were untreated, adult male CD-1 mice that had been housed in isolation for 6 to 10 weeks to enhance aggressiveness (*8*). The encounter was in a wooden arena 30.3 by 33.0 by 15.0 cm. The subject and opponent were placed together in the arena and allowed to interact until the test animal submitted. An animal was considered to have submitted when it (i) displayed the characteristic upright submissive posture, and (ii) failed to fight back when subsequently attacked by the opponent (*9*).

The mice then were randomly assigned to one of three control groups or one of three experimental groups (8 to 11 per group). Immediately after the initial defeat, all mice received a single injection. The mice in the control groups received a subcutaneous injection of 0.05 ml of saline (placebo), whereas those in the experimental groups received a subcutaneous injection of 2 I.U. of ACTH (Cortrophin-Zn, Organon) in 0.05 ml of saline. This dosage of ACTH was selected because it is effective in modifying avoidance responding in mice (*10*).

The mice in one experimental and one control group were tested for submissiveness with a novel opponent at one of three times: 24, 48, or 168 hours after the initial defeat and hormone or placebo treatment. The test of submissiveness was conducted as was the encounter for the initial defeat: The test an-

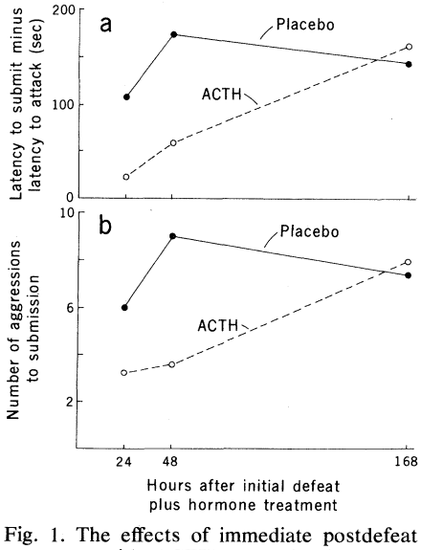

Fig. 1. The effects of immediate postdefeat treatment with ACTH or a placebo on (a) mean latency to submit minus latency to attack at each postdefeat interval, and (b) mean number of aggressions to submission at each postdefeat interval.

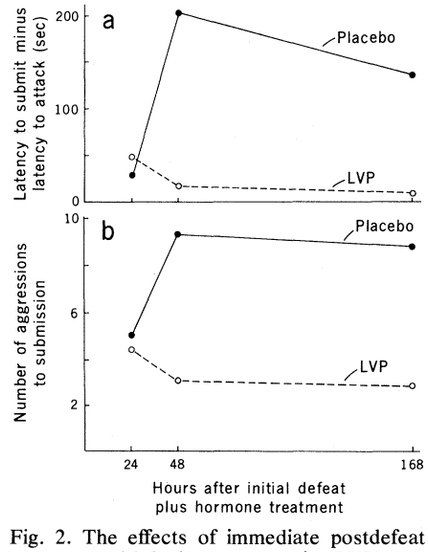

Fig. 2. The effects of immediate postdefeat treatment with lysine vasopressin (*LVP*) or a placebo on (a) mean latency to submit minus latency to attack at each postdefeat interval, and (b) mean number of aggressions to submission at each postdefeat interval.

0036-8075/79/0622-1343$00.50/0

imal and a novel opponent were placed in the wooden arena and allowed to interact until the test animal submitted. We used two measures to assess submissiveness during this test. The first, the latency to submit minus the latency to attack, was defined as the duration of the interval between the opponent's initial attack and the subsequent submission by the test animal. According to this measure, the shorter the interval, the more submissive the test animal. The second measure was the number of aggressions or attacks by the opponent needed to induce submission in the test animal; here, the fewer attacks required, the more submissive the test animal.

Administration of ACTH immediately after the initial defeat led to increased submissiveness in the mice tested at 24 or 48 hours, but not in those tested at 168 hours (Fig. 1). This effect was apparent in both measures of submissiveness used, the latency to submit minus the latency to attack ($P < .06$, by analysis of variance) and the number of aggressions to submission ($P < .01$). Thus, increasing ACTH levels after an initial defeat leads to increased submissiveness in future competitive encounters, and this effect lasts for at least 48 hours but not for 7 days.

The second experiment examined the effects of postdefeat treatments with lysine vasopressin on future submissiveness. The design of this experiment was identical to that of the first, except that the mice (8 to 11 per group) in the three experimental groups were treated with a single subcutaneous injection of synthetic lysine vasopressin (Nutritional Biochemicals Corp.), which was administered at a dosage of 0.08 I.U. in 0.05 ml of saline. This dosage was selected because it has marked effects on avoidance responding in mice (*3*).

In this second experiment, postdefeat treatment with lysine vasopressin led to increased submissiveness in those mice tested at 48 or 168 hours, but not in those tested at 24 hours (Fig. 2). Again, this effect was reflected in both measures of submissiveness used ($P < .01$ for both). However, the control mice tested at 24 hours were quite submissive, and thus a "ceiling effect" may have precluded seeing any effects of vasopressin at this testing time. Therefore, this study shows that increasing vasopressin levels immediately after an initial defeat leads to increased submissiveness in future encounters, and that this effect, once evident, persists until at least 7 days after the initial experience.

These two studies show that increasing the levels of the pituitary peptides ACTH and vasopressin immediately after an initial defeat leads to increased submissiveness in future competitive situations. Because submissive responses can be viewed as naturally occurring avoidance reactions (*11*), these findings are consistent with earlier studies of laboratory-specific avoidance responses in showing that raising the levels of these hormones after initial stressful experiences enhances later adaptive responding (*6*). Furthermore, the time courses of the effects of ACTH and vasopressin observed here are similar to those observed in earlier studies of avoidance behavior: ACTH exerts relatively short-lived effects, whereas those of vasopressin last much longer (*3, 12*). Thus, although ACTH and vasopressin have similar facilitative effects on adaptive responding, the time courses of their effects are different.

Because both ACTH and vasopressin levels normally increase following exposure to stressful stimuli (*13*), it seems likely that the techniques used in these studies produced a functional exaggeration of those normal peptide responses to stress. Therefore, we interpret the results of these two studies as supporting the suggestion (*1, 2, 4*) that the normal peptide hormone responses to initial stressful experiences in some way can facilitate the memory of those experiences, as reflected in future adaptive behavioral responses.

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1 February 1978; revised 2 November 1978

Intermediate-Disturbance Hypothesis

There is a tropical island ideally suited for testing Connell's (*1*) intermediate-disturbance hypothesis for tropical forest species diversity, upon which there are contrasting disturbed and undisturbed areas. Whitmore's (*2*) monograph on the forests of the Solomon Islands is an essay on disturbance by cyclones and the adaptation of tree species for different roles in the regeneration process. The cyclone-disturbed north coast forests of Kolombangara Island are dominated by relatively light-demanding tree species that are not reproducing themselves in the understory; shade-tolerant species are also present in lesser numbers. The relatively undisturbed west coast forests are dominated by fewer, more shade-tolerant species that are well represented in the understory. The number of tree species scarcely differs between the north and the west coasts (129 versus 122, respectively), but species diversity is greater in the cyclone-disturbed north coast forests (.898 as against .715 on the west coast) (*3*). The noticeably greater evenness of representation of species in the disturbed forests accounts for this. This comparison is especially suitable because it demonstrates the effect of disturbance in ecological time on an island where the species pool is the same for both sample areas (evolutionary changes are discussed below). In this instance, the difference in number of species is disappointingly small, but this might be related to the position of these communities on a scale of disturbance relative to dynamic stability (*4*).

Connell's (*1*) dated reference to the

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