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Behavioral and Physiological Effects of Capsaicin in Red-Winged Blackbirds

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MASON, J. R. AND J. A. MARUNIAK. *Behavioral and physiological effects of capsaicin in red-winged blackbirds.* PHARMACOL BIOCHEM BEHAV 19(5) 857–862, 1983.—We injected red-winged blackbirds *(Agelaius phoeniceus)* subcutaneously with capsaicin, and assessed (a) changes in basal body temperature, (b) ability to discriminate warm from cool drinking water, and (c) sensitivity to oral and topical applications of capsaicin, a trigeminal irritant. As predicted from studies of mammals, the injections seemed to disrupt thermoregulation when the ambient temperature increased, and eliminated discrimination between warm and cool drinking water (Figs. 1 and 2). In contrast to effects on mammals, injections failed to observably diminish oral or topical sensitivity to capsaicin and apparently induced a capsaicin preference in two-bottle drinking tests between capsaicin and its vehicle (Fig. 3). Such preferences were context-dependent, however, since water was reliably preferred to capsaicin or vehicle in three-bottle tests. To our knowledge, the present work is the first to report physiological and behavioral effects of capsaicin on birds, and the first to suggest that the substance may have different behavioral and physiological effects on different classes of animals.

Blackbirds Capsaicin Trigeminal Taste Thermoregulation Temperature Discrimination

CAPSAICIN, the pungent ingredient in peppers of the Capsicum family, has wideranging physiological effects on mammals that include impaired thermoregulation [18] and heat discrimination [11, 12, 27, 28], virtual elimination of responses to nociceptive chemical stimuli [14,17], and elevated thresholds for evoked responses to photic and acoustical stimuli [30]. Examination of capsaicin congeners has suggested that structural characteristics of the vanillyl, acylamide and alkyl chain moieties of capsaicin molecules determine potency [42], and that capsaicin molecules interact with a molecular recognition site which discriminates subtle differences in ligand structure [25]. Capsaicin acts by causing the dose-dependent release and depletion of substance P from primary sensory neurons [8, 9, 16, 19]. Adult rats given capsaicin neonatally have reduced numbers of sensory ganglia neurons and suffer destruction of fibers in peripheral nerves and dorsal roots [10,43].

Because capsaicin impairs trigeminal chemoreception in mammals, it has been used as a tool for the study of interactions between the trigeminal system and other chemosensory systems for the perception of volatile stimuli [40]. Presumably, olfactory and/or vomeronasal cues alone mediate responding to odorant volatiles in capsaicin-desensitized mammals. Unlike mammals, birds lack a vomeronasal system [29], and thus, they represent an ideal model for study of olfactory trigeminal interactions. Both the oral and nasal cavities in birds are well-supplied by the trigeminal nerve (e.g., [1,46]), and there is little doubt that trigeminally-mediated information has at least some behavioral significance [21,23]. If capsaicin were to eliminate trigeminal chemoreception in birds as it does in mammals, then capsaicin desensitization might be used for study of the essentially isolated olfactory responses of birds to volatile stimuli. To our knowledge, however, no information is available regarding the effect(s) of capsaicin on the avian trigeminal system. Although one might expect birds to respond to trigeminal irritants (e.g., capsaicin, ammonia) in a manner generally similar to mammals, dissimilar responses have been observed in some avian species. Pigeons *(Columba livia)* and grey partridges *(Perdix perdix)* appear insensitive to strong ammonia solutions (e.g., [41]), and parrots (e.g., *Lorius roratus)* normally eat Capsicum peppers (e.g., [33]). In contrast, no infrahuman mammal voluntarily consumes Capsicum peppers, and preferences for capsaicin or other severe trigeminal irritants cannot be induced [38]. Here, we report two experiments designed to assess whether subcutaneous injections of capsaicin would (a) affect basal body temperatures of red-winged blackbirds *(Agelaius phoeniceus),* (b) disrupt the birds' abilities to discriminate warm from cool drinking water, and (c) desensitize the birds to oral and topical presentations of capsaicin.

EXPERIMENT 1

Method

Twenty adult (mean weight 75±3.5 g) male red-winged blackbirds were decoy-trapped during August 1981 at Sandusky, OH, and brought to our laboratory 4 weeks before the experiment began. Each was individually housed (cage dimensions: 75×45×45 cm), and permitted free access to Purina Flight Bird Conditioner, grit, and tapwater presented in two 30 ml calibrated drinking tubes. A 6:18 light-dark cycle was used to maximize feeding and drinking without reducing the total amounts consumed [35]. One week before the experiment, each bird was visually isolated with cardboard sheets [22].

Following adaptation, the birds were tested for preferences between warm (42±0.3°C) and cool (23±2°C) drinking water on each of 4 successive days. Red-wings (like other birds, such as chickens) reliably discriminate temperature differences in drinking water of as little as 3.0°C, and, in contrast to rodents (e.g., [2]), reliably drink less of the higher temperature [21]. For the tests, the birds were water-deprived for 2 hours and then given 30 ml of warm water in one drinking tube and 30 ml of cool water in the other for 30 minutes. To maintain the temperatures of the water samples, the drinking tubes were insulated with styrofoam and aluminum foil. The mean decrease in the temperature of the warm water samples was 6.0±0.5°C over the 30 minute test periods, while the temperature of the cool water samples remained nearly constant. Both drinking tubes were concealed from the birds with cardboard sheets, and positioned 5 cm apart at the front of the cages. The positions of the tubes (and thus presentations of warm and cool water) were counterbalanced among birds and across days. Also, the basal body temperature of each bird was monitored daily by inserting a thermistor probe (Yellow Springs No. 401) 2–3 cm into the cloaca, and recording the temperature with a telethermometer unit (Yellow Springs No. 46TUC).

On the fifth day, the birds were randomly assigned to 4 groups. The birds in Group 1 were given 2 sub-cutaneous (SC) injections of 0.1% (w/v) capsaicin solution (0.23 ml, 0.48 ml, 1 injection/day) under the breast skin. The birds in Group 2 were given 4 injections (SC) (0.23 ml, 0.36 ml, 0.48 ml, 0.60 ml, 1 injection/day), and the birds in Group 3, 7 injections (SC) (0.23 ml, 0.23 ml, 0.36 ml, 0.48 ml, 0.60 ml, 0.75 ml, 0.90 ml, 1 injection/day) of capsaicin solution. The birds in Group 4 were given 7 injections (SC) of vehicle (0.23 ml, 0.23 ml, 0.36 ml, 0.48 ml, 0.60 ml, 0.75 ml, 0.90 ml, 1 injection/day), as a control. The capsaicin solution was prepared by dissolving 1 g of capsaicin in a vehicle solution of 10 ml ethanol, 10 ml Tween 80, and 80 ml 0.9% saline [17]. Interestingly, we observed few behavioral symptoms of distress in the birds following capsaicin injections. The major effects appeared to be intoxication, perhaps caused by the ethanol in the vehicle, and gastrointestinal malaise. Symptoms of intoxication were observed in both experimental and control birds after large (i.e., 0.75 ml, 0.90 ml) injections, and included wobbling, and unsteadiness and slipping when on perches. Malaise was suggested by beak wiping [3], although vomiting was never observed. In all cases, symptoms of intoxication and/or malaise disappeared within 30 minutes of injection. On the 5 days immediately following the last day of treatment for Groups 1 and 2, and on the 9 days following the last day of treatment for group 3, the birds were again tested for preferences between warm and cool water, and basal body temperatures were recorded. Birds in the control group (Group 4) were tested for preferences and their body temperatures were recorded on all days (Days 5–20).

Drinking scores in the water discrimination tests were converted into preference ratios (e.g., warm water consumption/total consumption). These ratios, as well as measurements of basal body temperature, were assessed by 2-way analyses of variance, with repeated measures on one factor. In such analyses, the independent factor was groups, while the repeated factor was days. For comparison of all groups, pre-treatment data and data collected on the five days following the last day of treatment were used. For comparison of Group 4 with groups 1 and 2 only, the appropriate Group 4 post-treatment data were selected (i.e., days 7–11 for comparison with Group 1; days 9–13 for comparison with Group 2. For Group 4 only, one-way repeated measures analyses of variance were performed to assess whether preference ratios or basal body temperatures changed over pre- and post-treatment days. In all cases, subsequent to analysis of variance, Tukey *b* tests [45] were used to isolate significant differences among means.

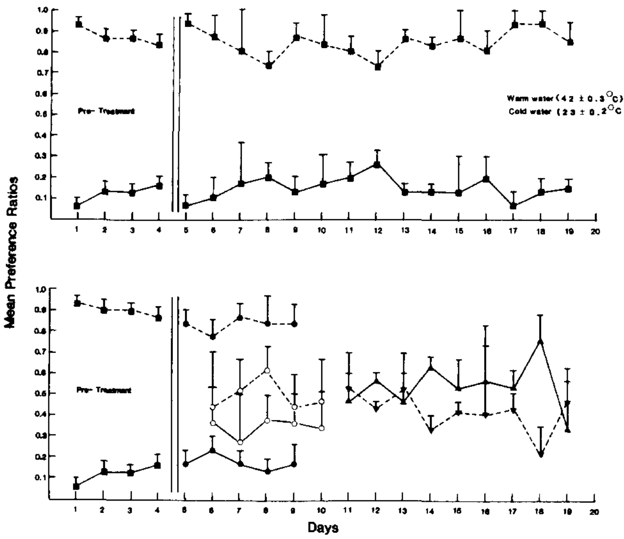

FIG. 1. (Panel A) Mean preference ratios for warm (dotted line) and cool (solid line) water exhibited before treatment. All birds preferred cool water ($p<0.05$). (Panel B) Mean preference ratios for warm (dotted line) and cool (solid line) water exhibited by control birds. Cool water was preferred before, during, and after treatment ($ps<0.05$). (Panels C, D, E) Mean preference ratios for warm (dotted line) and cool (solid line) water by birds given 2 (C), 4 (D) or 7 (E) injections (SC) of 1% capsaicin. While all these birds preferred cool water before treatment ($ps<0.05$), only birds given 2 injections of capsaicin showed such preferences after treatment. Capped vertical bars represent standard errors of the means.

Results

When all groups were compared, there were significant differences in preference ratios, $F(3,16)=8.8, p<0.05$, and a significant interaction between preference ratios and days, $F(21,112)=4.3$, $p<0.05$. Tukey tests indicated that before treatment, all groups preferred cool water ($p<0.05$). After treatment, only Group 1 (2 capsaicin injections) and Group 4 (7 control injections) exhibited such preferences ($ps<0.05$). Groups 2 and 3 (4 and 7 capsaicin injections, respectively) showed no preferences between warm and cool water ($p>0.25$) (Fig. 1).

When the post-treatment performances of Groups 1 and 2 were compared with appropriate data from Group 4 (i.e., performance on days 7–11 or 9–13, respectively), there were significant differences between Groups 2 and 4, $F(1,8)=6.2$, $p<0.05$. Group 4 exhibited preferences for cool water ($p<0.05$), while Group 2 showed no such preferences ($p>0.25$). There were no significant differences between Groups 1 and 4; both groups preferred cool to warm water. When preferences exhibited by Group 4 alone were examined across pre- and post-treatment days, no significant differences were found ($p>0.25$).

There were significant differences among groups, $F(3,16)=6.4, p<0.05$, and over days, $F(7,112)=3.8, p<0.05$, in basal body temperature, and the interaction between groups and days was significant, $F(21,112)=3.1$, $p<0.05$. Tukey tests indicated that, before treatment, there were no significant differences during pre-treatment among groups in basal body temperature ($p>0.10$). The mean body temperature of the birds was 43.9±0.4°C. After treatment, however, post-hoc comparisons indicated that there were significant changes in body temperature for Group 3 (7 capsaicin injections), and these changes varied over tests (ps<0.05). When these fluctuations in body temperature were correlated with uncontrolled fluctuations in the ambient temperature of the laboratory, a significant positive value was obtained (Spearman's $r=0.92$, $p<0.01$) (Fig. 2). There were no significant differences within or among Groups 1, 2, and 4 (2 capsaicin injections, 4 capsaicin injections, or 7 control injections, respectively) on any of the post-treatment days (ps>0.10). When Groups 1 and 2 were compared with Group 4, there were no significant differences in basal body temperatures (ps>0.25, respectively). When the basal body temperatures of birds in Group 4 only were examined across pre- and post-treatment days, no significant differences were observed ($p>0.25$).

Discussion

The results of the present experiment indicate that subcutaneous injections of capsaicin have several effects on red-winged blackbirds that are similar to those observed in rodents [14,28]. For example, relative to the other groups, birds in Group 3 (7 capsaicin injections) seemed less able to defend basal body temperature against increases in the ambient environmental temperature. This finding is consistent with evidence previously reported for rats [30]. Because the primary brain site responsible for regulation of body temperature is believed to be in the anterior hypothalamus [5,32], we suggest that capsaicin might have affected that structure and that such changes subsequently interfered with temperature regulation. Alternatively, it is known that the spinal cord is also involved in thermoregulation in birds [31], and therefore may have been the site of action of capsaicin in the present experiments.

Capsaicin injections also interfered with the bird's ability to make behavioral discriminations between warm and cool drinking water. Whether capsaicin also interfered with thermal sensitivity on other body surfaces (e.g., the feet) is unclear. However, capsaicin injected rats lose the ability to locate food on the basis of thermal cues transmitted through the floor of a maze [28]. Such inability may reflect depletion of neurotransmitter in and/or degeneration of oral thermoreceptors [30]. Capsaicin is believed to chronically deplete substance P and/or somatostatin from primary afferent neurons [16,17]. Moreover, administration of capsaicin to neonatal rats causes massive degeneration of primary afferent neurons. Such degeneration is very rapid, with the first signs appearing 30 minutes after treatment [25]. Because transmitter and receptor depletion are highly dependent on the dose of capsaicin administered [26], we hypothesize that the loss of thermal discrimination after 4 injections, and thermoregulation after 7 injections, are dose dependent phenomena, possibly reflecting differential neurotransmitter depletion and/or receptor degeneration.

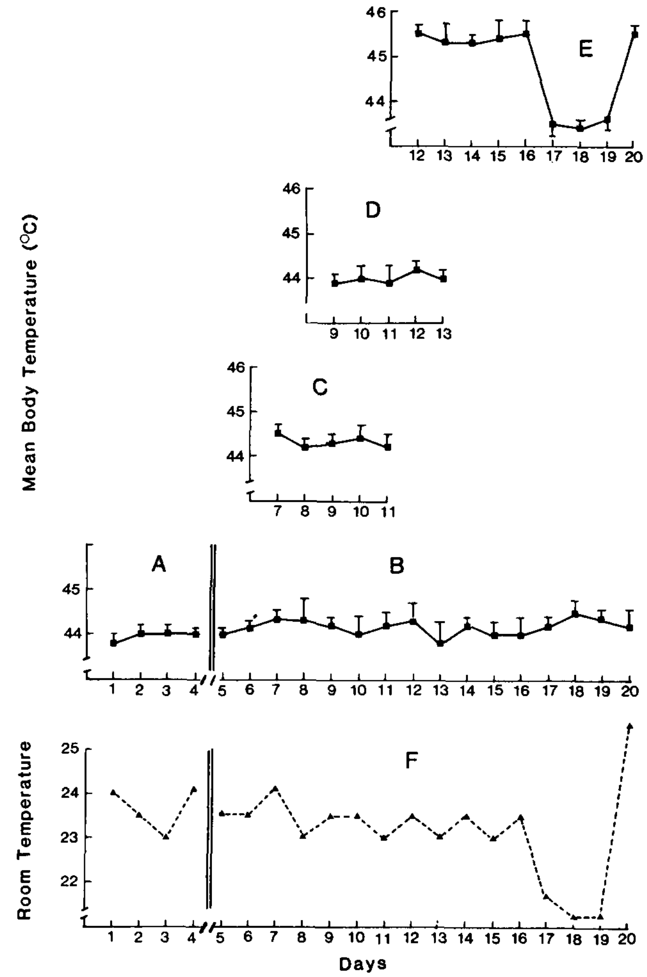

FIG. 2. (Panel A) Mean body temperatures of all birds regardless of group before treatment. (Panel B) Mean body temperatures of control birds during and after treatment. (Panels C, D, E) Mean body temperatures of birds given 2 (C), 4 (D) or 7 (E) injections of 1% capsaicin. There were significant fluctuations in body temperatures of birds given 7 capsaicin injections ($p<0.05$), and these fluctuations were positively correlated with uncontrolled changes in room temperature (Panel F; $p<0.01$). There were no changes in body temperature exhibited by birds in the other groups. Capped vertical bars represent standard errors of the means.

Unlike mammals (e.g., [14]), the red-wings did not become insensitive to capsaicin after injection. Even after 7 injections of capsaicin solution, the red-wings reacted (e.g., sustained eye blinks, head shaking) to 5% capsaicin or ammonia solutions placed on their eyes. Capsaicin treated rats do not react to such applications [15]. In Experiment 2, we investigated whether capsaicin treated birds might also remain sensitive to oral presentations of capsaicin.

EXPERIMENT 2

Method

The subjects were 30 male red-winged blackbirds (mean weight 73±2.6 g) obtained, housed and adapted to laboratory conditions as previously described.

Following adaptation, the birds were randomly assigned to 3 groups. The birds in Groups 1 and 2 were given 7 injections (SC) of 1% (w/v) capsaicin solution in the following daily fractions: 0.23 ml, 0.23 ml, 0.36 ml, 0.48 ml, 0.60 ml, 0.75 ml, 0.90 ml. The birds in Group 3 were given 7 injections (SC) of vehicle in the same daily fractions as Groups 1 and 2. On the 8 days immediately following the last day of treatment, Groups 1 and 3 were given completely counterbalanced 2 bottle drinking tests between 5% capsaicin solution and vehicle. Group 2 was given counterbalanced 3 bottle drinking tests between 5% capsaicin solution, vehicle and tapwater to assess the relative preferences of birds for capsaicin or vehicle when water was also available. Presentations of the tubes to the birds was as described in Experiment 1. The amount consumed from each bottle was recorded 30 min, 60 min, 120 min, and 24 hr after presentation. Observation of the birds suggested that little spillage occurred, and we believe that our measures accurately reflected ingestion.

The data were converted into preference ratios (e.g., for Group 1 and 3, amount of capsaicin solution consumed/total consumption of capsaicin and vehicle). Tapwater consumption by Group 2 was not analyzed, per se, because our interest was in how much capsaicin and vehicle were consumed when tapwater was also available. Preference ratios were assessed by 2-way analysis of variance with repeated measures on one factor. The independent variable in the analysis was groups and the repeated factor was days. As in Experiment 1, Tukey *b* post-hoc comparisons were used after analysis of variance to identify significant differences among means.

Results

There were significant differences in preference ratios among groups, $F(2,27)=7.0, p<0.05$. Tukey *b* tests indicated that Group 1 showed preferences (relatively high ratios), and Group 3 showed rejection (low ratios) for capsaicin (Fig. 3, $ps<0.05$). Group 2 was indifferent (exhibited intermediate preference ratios); apparently, these birds preferred tapwater. Within groups, there were no differences across days in preference behavior ($p>0.25$).

Discussion

The results of Experiment 2 indicated that capsaicin injections did not disrupt oral sensitivity to capsaicin. The birds in all 3 groups continued to respond differentially to the substance, regardless of treatment. Group 3 avoided capsaicin, preferring vehicle; Group 2 avoided consumption of either capsaicin or vehicle, apparently preferring tapwater; and Group 1 avoided consumption of vehicle, instead displaying a weak preference for 5% capsaicin solution. These findings are contrary to those reported for mammals and conflict with observations obtained in our own laboratory in which rats were given identical treatments to those reported here (Mason and Maruniak unpublished observation). In general, capsaicin injections desensitize rats to oral presentations of capsaicin, and such animals exhibit equal consumption of capsaicin solution and vehicle.

A surprising result is that Group 1 showed weak preferences for capsaicin. Besides humans, who develop positive responses to chili peppers (e.g., [36,38]), and some parrots, who consume chili peppers as part of their normal diet, no other animals apparently show preferences for the substance, either as a result of exposure or training [7,37]. The induced preferences we observed were context dependent, however, and tapwater was preferred when it was presented as an alternative to capsaicin solution or vehicle. Such context dependence is not well-understood, but it is commonly observed among birds in taste experiments, regardless of the stimuli presented [20]. Whether the results of 2-choice tests reflect a change in the "taste" of capsaicin or a "hedonic shift" for capsaicin [38] even though its "taste" remained constant is unanswerable from data collected in the present experiment.

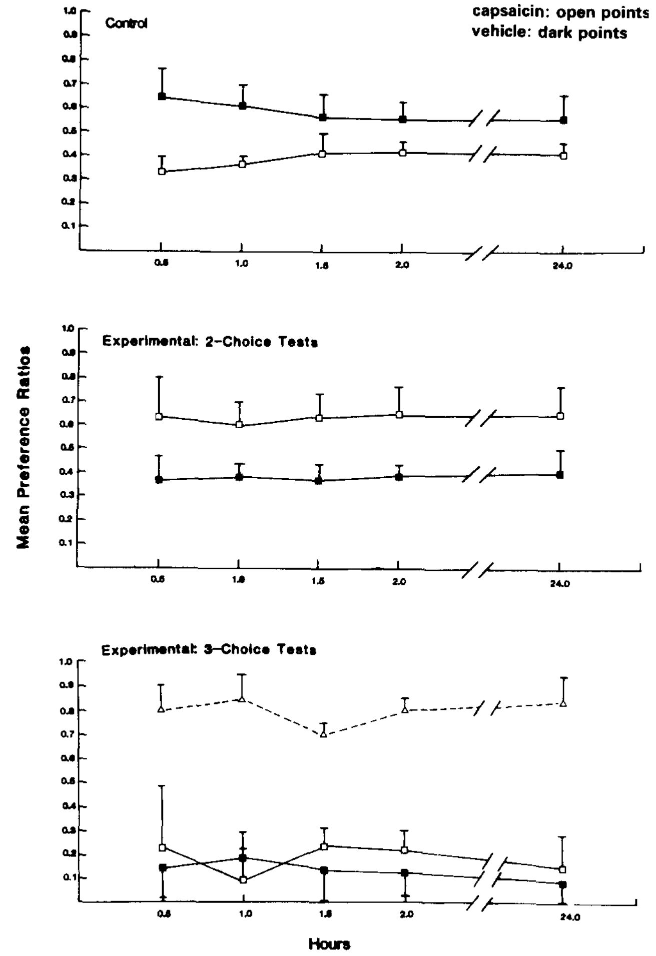

FIG. 3. (Top panel) Mean preference ratios for consumption of 5% capsaicin solution or vehicle by control birds (Group 3) after 0.5, 1.0, 1.5, 2.0, and 24 hr, over eight days of testing. Vehicle was always preferred ($ps<0.05$). (Middle panel) Mean preference ratios for consumption of 5% capsaicin or vehicle by Group 1 experimental birds (2-bottle tests) after 0.5, 1.0, 1.5, 2.0, and 24 hr, over eight days of testing. Capsaicin was preferred ($p<0.05$). Capped vertical bars represent standard errors of the means. (Bottom panel). Mean preference ratios for consumption of 5% capsaicin, vehicle, or water by Group 2 experimental birds (3-bottle tests) after 0.5, 1.0, 1.5, 2.0, and 24 hr, over 8 days of testing. There were no differences between consumption of vehicle and capsaicin ($p>0.25$). Tapwater (dotted line) was apparently preferred. Capped vertical bars represent standard errors of the means.

GENERAL DISCUSSION

The results of the present experiments show that subcutaneous injections of capsaicin disrupt heat discrimination and thermoregulation in birds, but not oral (and topical) sensitivity for capsaicin. The results are similar to those obtained with rodents for disruption of heat discrimination and thermoregulation, but contrary to results obtained for oral and topical sensitivity. Systemic injection of capsaicin into rats or guinea pigs produces a chronic desensitization to chemical irritants [13], and the animals do not respond to capsaicin, ammonia or other irritants on their eyes [15]. Also, rats who reliably avoid diets containing chili pepper become indifferent to such diets after systematic desensitization with capsaicin [37]. Conversely, the red-wings exhibited preferences for capsaicin in 2-bottle tests (i.e., reversal of unlearned aversions) and showed symptoms of discomfort when the capsaicin was placed on their eyes, or on their feet, despite injections of high doses of capsaicin. We do not believe that the capsaicin preferences observed in the 2-bottle tests were actually aversions for the taste of the vehicle, reinforced, for example, by ethanol-induced malaise [6]. Control group birds preferred vehicle to capsaicin, even though they had also experienced ethanol-induced malaise. A plausible explanation of the results is that the gradual exposure to increasing levels of either capsaicin or ethanol was sufficient to reverse initial aversions for these substances [36,41]. Simple exposure to initially aversive tastes [4,44] can be sufficient for induction of preference behavior, and a few strains of mice [24], and some individual rats [34] come to show preferences for ethanol in water after several exposures. However, to our knowledge, the present work is the first report that birds exhibit preferences as a function of exposure and the first evidence that exposure to capsaicin, at least under specific circumstances, can induce preference behavior in an infrahuman species [38]. Nonhuman animals can rarely be induced to show any sort of preference for an innately unpalatable substance (although innately palatable substances can become aversive via conditioned taste aversion learning [38]), and besides the present work, there is no evidence to suggest a hedonic shift, from negative to positive, for such substances. If an hedonic shift did occur, one explanation might be that the birds were reinforced by the physiological consequences of capsaicin ingestion. Silver and Maruniak [39] have proposed that capsaicin elicits the secretion of enkephalins and endorphins, triggered by the release of substance P. However, this explanation would require that the prior injections of capsaicin either did not cause chronic depletion of substance P in primary afferent neurons and/or neuronal degeneration, or responses to oral stimulation produced by capsaicin were mediated by receptors not affected by the injections.

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