would fall when (unbound) ACh was depleted; this, in turn, would favor passive carrier-mediated transport of choline into the ending under the influence of an electrochemical gradient (*14*) even if the extracellular concentration of choline were considerably less than the cytoplasmic concentration. An apparent change in high affinity choline uptake under the conditions used could also occur as a result of drug-induced changes in the isotopic dilution of labeled choline by endogenous choline, although Simon and Kuhar (*5*) have stated that endogenous choline levels in the incubation medium "were extremely low and no difference was found between synaptosomal fractions from pentobarbital treated animals and those from control animals." For these reasons, choline concentrations in both the synaptosomal pellet and the incubation medium were measured and are reported in Table 2. The synaptosomal choline concentration and mole fraction of [$^2H_4$]choline were not significantly changed by any of the treatments. It may nevertheless be fallacious to infer from these results that the choline concentration within cholinergic nerve endings does not change under these experimental conditions. While it seems reasonable to suppose that most of the ACh is contained in cholinergic synaptosomes and therefore reflects cholinergic function, choline is a universal constituent of all cells and there is evidence that concentrations of endogenous and isotopic choline in whole brain (or parts of it) may not be representative of those in cholinergic nerve endings (*15*). The constant synaptosomal choline concentrations which we report do not therefore preclude the occurrence of adaptive changes in choline concentration in cholinergic endings in response to changes in ACh turnover rate and concentration.

The concentration of endogenous choline found in the supernatant was less than 0.04 μM, which is unlikely to influence these experimental results significantly; however, this would be sufficient to obfuscate the interpretation of experiments in which lower concentrations of [^3H]choline are used and endogenous choline concentration in the supernatant is not measured.

In summary, we have shown that changes in high affinity choline uptake by synaptosomes which appear to result from experimental manipulation of cholinergic activity before the animal is killed are associated also with changes in synaptosomal ACh content and turnover. The simplest mechanism for modulation of choline uptake by antemortem neuronal activity appears to be an effect of synaptosomal ACh concentration on high affinity choline uptake. Whether this is a direct effect on ACh or is due to a secondary change in synaptosomal choline levels remains to be established.

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15. For example, NH_4^+ appears to reduce substantially the amount of [^2H]choline entering the brain following an intravenous injection without altering the rate of [^2H]ACh synthesis [S. H. Butcher, L. L. Butcher, A. K. Cho, *Life Sci.* **18**, 733 (1976)], suggesting an effect of NH_4^+ on the nonspecific component of choline uptake which is not associated with ACh synthesis. Others have reported that cholinergic denervation of the hippocampus results in little or no reduction in the entry of [^3H]choline, despite other evidence of degeneration of cholinergic terminals [V. H. Sethy, R. H. Roth, M. J. Kuhar, M. H. VanWoert, *Neuropharmacology* **12**, 819 (1973); Atweh and Kuhar (*10a*)]. There is also evidence that choline is compartmentalized in synaptosomal preparations [P. G. Guyenet, P. LeFresne, J. C. Beaujovan, J. Glowinski, in *Cholinergic Mechanisms*, P. G. Waser, Ed. (Raven, New York, 1975), p. 137].
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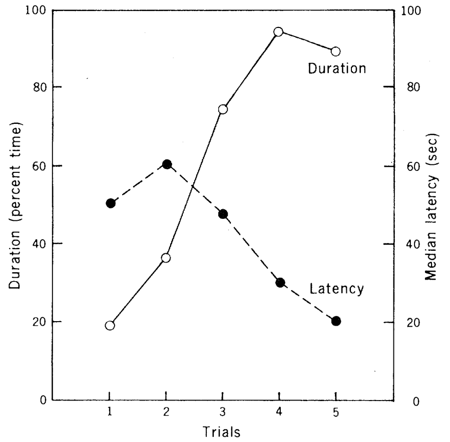
Tail-Pinch Stimulation: Sufficient Motivation for Learning

Abstract. *A paper clip applied to the tails of rats induced gnawing and eating, which decreased in latency and increased in duration with experience. With sustained pressure to the tail, rats learned a new habit in order to gain access to wood chips on which to gnaw. That these are also properties of behavior elicited by electrical brain stimulation suggests that both manipulations may act through the same mechanism. These results support the hypothesis that a nonspecific arousing stimulus can be a sufficient condition for establishing learned habits.*

Mild pressure to the tails of rats elicits eating, gnawing, biting, and licking (*1*), which resemble behaviors elicited by electrical stimulation of the hypothalamus (*2*). The particular behavior elicited by tail-pinch depends on the particular goal object available (*3*); this is also true of electrically induced behavior (*4*). Further similarities between behavior elicited by tail-pinch and that elicited by hypothalamic stimulation can be discovered by examining the learning that contributes to the plasticity of the behavior.

Electrically induced behavior appears gradually and requires some experience with the stimulation before a reliable response can be elicited (*5*); the strength of this response increases with additional experience with the stimulation (*5*). In addition, when the hypothalamus is stimulated, an animal will learn a new approach response that will allow it to perform the appropriate consummatory behavior (*6*). In the presence of electrical brain stimulation, animals will learn to find a variety of appropriate objects with which to engage in consummatory behavior. Cats learned a Y-maze in order to attack a rat during hypothalamic stimulation (*7*). Satiated rats receiving hypothalamic stimulation learned the new



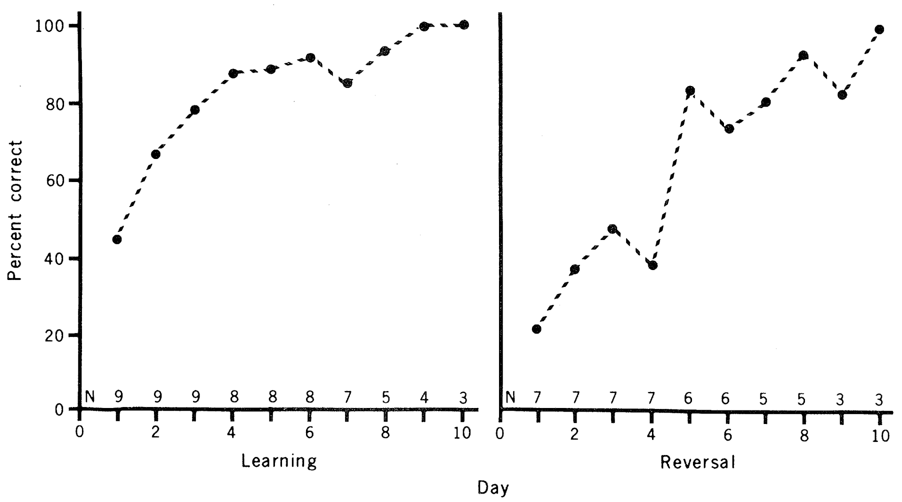


Fig. 1 (left). Median latency of ten rats to start gnawing food pellets in response to a tail-pinch, and median duration of gnawing (percentage of available time spent gnawing for at least 10 seconds).

Fig. 2 (right). Total percentage of correct responses in the first ten sessions of learning a T-maze to obtain the opportunity to gnaw on wood during tail-pinch. Nine rats learned the criterion of nine out of ten correct responses in two successive sessions of five trials each.

response of pressing a lever for food (*8*), learned a T-maze for food (*9*), and learned a Y-maze in order to gnaw on a board (*10*).

We now report that (i) experience plays an important role in modifying tail-pinch behavior, and (ii) rats with their tails pinched will learn a T-maze in order to obtain the opportunity to gnaw on wood. Our results indicate that a nonspecific arousing stimulus can induce animals to perform an instrumental response to obtain an appropriate goal, and we suggest that the similar nonspecific arousing properties of electrical brain stimulation may have a role in producing the behavior elicited by such stimulation.

Twelve female hooded rats approximately 120 days old, housed in two groups of six, with free access to food and water, were studied. In experiment 1, the acquisition of behavior induced by tail-pinch was measured in an open field (78 by 43 cm) littered with food pellets. After a 2-minute habituation period, a paper clip 7.8 by 1.8 cm and padded with plastic tape was applied 4.0 to 4.5 cm from the tip of the tail; it was removed 2 minutes later. The clip was suspended by elastic from a runner on a curtain rod in order to keep the tail off the floor and still allow freedom of movement. In this way, the rats could be prevented from biting the clip. The rats ran around the open field in short bursts, sometimes vocalizing, picking up food pellets and chewing them. Sometimes they ingested the food and sometimes they merely shredded it. The latency of gnawing the food and the length of time spent gnawing were recorded. Each rat was tested once on each of 5 days within a 10-day period (Fig. 1). The data of two rats that failed to gnaw for at least 10 seconds on any trial are not included. The latency of gnawing decreased significantly with experience (*11*), which confirmed an earlier observation (*12*). Once the rats had started to gnaw, the proportion of the remaining time spent gnawing increased significantly (*11*), which suggests that the rats had learned to gnaw by experience.

For experiment 2, a roofless T-maze 30 cm high was constructed of unpainted aluminum. A start box (21 by 10 cm) led to two arms (25 by 10 cm) that led to goal boxes (30 by 10 cm). The curtain rod, with the paper clip attached by elastic, ran the length of the two arms. Pieces of wood were placed in one of the goal boxes in such a way that they could not be seen from the arms of the maze. For half of the rats, the wood was in the left goal box, and for the other half, it was in the right one. Each of the ten rats from experiment 1 received one five-trial session each day. A trial was started by attaching the paper clip (as in experiment 1) and placing the rat in the start box, where it was confined for 5 seconds by a door. The door was removed, and the rat was allowed to move freely through the maze. If it did not reach either goal box within 55 seconds, it was removed and the clip was taken off. If it reached either of the goal boxes, it was confined there for 30 seconds before being removed. At no time was the rat allowed to chew on its tail or on the clip. The intertrial interval was approximately 30 to 60 seconds. The rats were tested in a random order each day between 1600 and 1900 hours. The learning criterion was the choice of the goal box containing wood a total of at least nine times in two successive sessions. Once a rat had reached the criterion, the wood was placed in the other goal box on succeeding trials; reversal training was given until the same criterion was met.

Nine rats learned the maze in 15 to 80 trials (median, 40 trials). One rat seldom moved from the choice point in 100 trials, and its data are not included. Seven of the remaining rats reversed the habit in 20 to 100 trials (median, 40 trials). One rat became ill and died before reaching the criterion, and another stopped running the maze and did not learn the reversal within 100 trials; their data are not included. During learning, the rats improved by the third session from performance at chance level (P = .72) to a significant preference (P = .01) for the goal box with wood in it (Fig. 2) (*13*). All the rats gnawed wood on almost every trial when they reached the goal box; on their last five trials during learning and reversal, they spent an average of 74 and 82 percent, respectively, of the available time gnawing. Rats that ran to the incorrect goal box characteristically vocalized, defecated, and chased their tails.

The parallel between our findings and those of studies with electrical stimulation of the hypothalamus suggests a common mechanism of action. Valenstein (*4*) has suggested that hypothalamic stimulation may induce nonspecific arousal rather than activate specific drives. In its presence, rats learn to make appropriate responses to objects in the environment. According to Valenstein (*14*), the particular response is determined by several internal and external factors (such as the somatic, visceral, and motivational effects of the stimulation) as well as by environmental factors and species-specific characteristics. Tail-pinch may be regarded as a relatively nonspecific arousing stimulus, in the presence of which, rats learn to direct their behavior toward the environment. The particular response observed during tail-pinch may be determined by factors similar to those for brain stimulation. With both procedures, oral responsiveness increases in a way that is modified by experience with particular objects in the environment.

The finding that a relatively nonspecific stimulus can induce rats to learn a new habit in order to obtain an appropriate goal object for consummatory behavior has implications not only for interpreting behavior elicited by electrical brain stimulation but also for elucidating the conditions necessary for all learning. Indeed, several theorists have suggested that arousal may be a sufficient condition for learning (*15*). Thus, a general activation of some nonspecific arousal system within the brain would increase an organism's responsiveness to environmental stimuli and facilitate appropriate responses. The relative importance of species-typical response constraints and the role of specific neuronal circuitry are areas for future investigation.

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Threshold Model of Feeding Territoriality and Test with a Hawaiian Honeycreeper

Abstract. *A model is proposed predicting that in nectarivorous birds territorial behavior will occur above a lower threshold of nectar productivity in a foraging area and disappear above an upper threshold. These thresholds are determined by the daily costs of living of territorial and of nonterritorial individuals and by the pressure of competing birds for the resource. Decline of efficiency of territorial exclusiveness is predicted as productivity increases from the lower to the upper threshold. Hawaiian honeycreepers (*Vestiaria coccinea*) supported the model.*

The study of territoriality—herein defined as the maintenance of an area "within which the resident controls or restricts use of one or more environmental resources" (*1*)—has been characterized by a lack of tests of theoretical predictions (*2*). In this study we have applied a model to the energetic economics of feeding (nonbreeding) territoriality in a nectar-eating passerine bird, endemic to the Hawaiian Islands. The model predicts the conditions that determine the presence or absence of feeding territoriality in this species.

Ecologists (*2, 3*) have suggested some of the factors that should determine whether feeding territoriality in birds, involving costly defense and chasing, is economically feasible. Assuming that energy is potentially limiting, only under certain circumstances will the benefit of territoriality exceed the cost and will the establishment of a territory be favored. Conversely, if energy is not limiting, territorial behavior confers no energetic advantage and should cease to exist. Various studies (*4*) of flower-feeding hummingbirds suggested the overriding importance of high energy content of the resource (floral nectar) in territorial establishment. Likewise the number of inflorescences available seems (*5*) to determine territoriality in an African sunbird, as territories always included approximately the same number of flowers. Such environmental parameters as dispersion of food sources and number of competitors have little effect on the estimated energetic cost of territorial behavior in a Hawaiian honeycreeper (*6*). However, our present study shows that the number of inflorescences and the intruder pressure together determine the energetic yield of the territory to its owner, and therefore can be used to predict accurately the presence or absence of territoriality even though these parameters have little effect on territorial cost. Although one pioneering study (*5*) has quantitatively predicted and partially documented changes in territorial behavior based on economics, to our knowledge a thoroughly quantified test of this idea has yet to be accomplished.

Under conditions of potential food limitation, an animal should be able to raise the level of food availability in its foraging area by preventing other individuals from using its food supply. This prevention involves cost, including energy spent advertising or chasing (or both). If the added cost of living territorially equals or exceeds the resultant increase in energy availability, territorial behavior should not occur. The minimum energetic productivity (calories produced on a territory over 24 hours) required to favor territorial behavior should be predictable on the basis of (i) energetic yield to a nonterritorial individual, (ii) increase in yield to a territorial individual, and (iii) added cost of being territorial. This can be expressed in the following terms

$$E + T < aP + bP$$

That is, in order for territoriality to occur, E (basic cost of living) plus T (added cost of being territorial) must be less than the yield to the individual if nonterritorial (fraction a of productivity P) plus the extra yield gained by the individual if territorial (fraction b of productivity P). The value of the term bP will depend on the efficiency e of the territorial owner at restricting use of P, and therefore bP can be expressed as:

$$e\,(1 - a)\,P$$

where e is the fraction of intruders excluded by the owner.

As P becomes large, e can become gradually smaller, and the total energy costs of the territory owner will still be met. Eventually P may reach a value that satisfies the energy requirements of the owner, even given zero efficiency at excluding intruders. At very high values of P, then, territoriality should not occur. As P decreases below such high levels, an upper threshold for territoriality should be reached when

$$aP < E$$