monkeys indicated their preferences by falling or rolling in the direction of the correct food well. The reward was then placed in the monkeys' mouths by the experimenter.

Finally, three of the four monkeys underwent amputation of frontal poles and resection of dorsolateral frontal granular cortex back to the two limbs of the arcuate sulcus. There were no apparent additional neurological signs and the expected pacing was delayed 1 to 5 months in appearing. This time there was a pronounced retardation in relearning the delayed response. Nevertheless, every monkey eventually succeeded in returning to the preoperative level of efficiency (Table 1). Careful observation of the mode of solution revealed that positioning in front of the baited food well was used in every case.

As a control, the fifth monkey, B, underwent bilateral resection of frontal granular cortex uncomplicated by peripheral lesions. His relearning scores on the delayed response were quite comparable to those of the three monkeys with peripheral deprivations, certainly no worse. An attenuated disturbance might have been expected in those monkeys receiving repeated tests. This suggests that overtraining on the delayed response did not protect the monkeys from the effects of frontal resections. In contrast, earlier work had indicated that overtraining on visual discriminations protected monkeys from the effects of infero-temporal neocortical resections (3).

The remaining two monkeys, M and 4, derived from another experiment and reported here for comparative purposes, underwent multiple transection of frontal granular cortex. The knife cuts were about 2 mm apart and arranged in the form of a grid. Sperry's surgical technique was employed (4). The purpose was to determine whether horizontal intracortical interconnections are those responsible for successful performance of delayed response. In the context of the present experiment, this represented another attempt to mimic the effects of frontal resection. Both monkeys showed almost perfect retention of delayed response, and there was no evidence of the hyperactivity so characteristic of the frontal lobectomized monkey. This lack of effects should be contrasted with those following multiple transection of infero-temporal neocortex (5).

Delayed alternation has been used interchangeably with delayed response

as a test of immediate memory. There is some evidence that certain non-delay features distinguish the two tests in requirements for solution (6). We offer the following additional suggestive evidence. The four monkeys with frontal resections were unable to acquire the delayed-alternation habit within the limits of testing (2000 trials), whereas they did succeed in relearning the delaved response. Though the delay feature is common to both tests, delayed alternation alone seemed to be beyond the scope of the frontal operates.

To complete the evidence, the two monkeys with multiple frontal transections succeeded in acquiring the delayed-alternation habit within normal limits. And all seven monkeys acquired a simple color discrimination in 90 trials or less, within normal limits.

These results, taken together, suggest that proprioception may be more critically involved in the solution of delayed alternation than in delayed response, and that the frontal operate may depend upon positioning in order to succeed on the delayed response. In the broadest sense, the various sense modalities probably contribute to the solution of delayed response, and no unithe modality deprivation mimics the effects of frontal resections, though both visual and auditory discrimination may be impaired (1, 7). Unimodality deprivations are ineffective because of the multiplicity of solutions available to monkeys. As in the maze-learning experiments on rats (8), combined sensory deprivations will probably prove to have a more deleterious effect than unimodality deprivations (9).

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Relative Reinforcement Values of Food and Intracranial Stimulation

Abstract. Rats trained in a discrimination-reversal situation with either food pellets or intracranial stimulation as the reinforcing stimulus were not appreciably different in their first-task performance, but reversal training was slower if the first discrimination was learned with brain stimulation.

When utilized as a positive reinforcing stimulus, intracranial stimulation (ICS) has proved capable of maintaining high rates of responding in free operant situations under continuous reinforcement (1). Animals also perform satisfactorily in trial-by-trial maze and obstruction situations where intracranial stimulation is the reinforcer (2). Although it is now clear that intracranial stimulation is similar to other known reinforcers in many respects-for example, reinforcement schedule effects (3, 4)—there persists the opinion among many workers that ICS-reinforced behavior is less permanent than behavior conditioned with, say, food as the reinforcer.

The actual evidence for this assumption is scanty. Many investigators have informally reported difficulties in establishing and maintaining free operant responding when intermittent reinforcement is employed. Indeed, only short variable interval and fixed-ratio values appear to have been used with any degree of success in cats and rats (3), although success in getting some monkeys to work under extended values of fixed-ratio schedules has been reported (5). In the straight alley situation, extinction of ICS-reinforced running appears to be extremely rapid (6); and in mazes, there appears to be more overnight retention loss by ICS-reinforced than by food-reinforced rats (2).

The present experiment represents an attempt at a direct comparison of the relative permanence of behaviors conditioned with food and with ICS reinforcement. Male rats of the Sprague-Dawley strain were stereotaxically implanted with bipolar electrodes aimed at the posterior hypothalamus. The effectiveness of intracranial stimulation was then tested in a bar-pressing situation, and animals were discarded if they failed to respond consistently under continuous reinforcement conditions within 30 minutes. All animals, in all phases of the experiment, received the same stimulation: 0.5-second train of biphasic rectangular waves, at a frequency of 100 per second, and having

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a pulse duration of 0.1 msec and a current of 2.0 ma.

All animals were allowed a total food intake of 10 g of Purina chow per day. Animals were next trained to push open translucent panels in a Y-shaped, twochoice discrimination apparatus. Each animal received pretraining with both food pellets and intracranial stimulation, and with the left and the right panels being both dark and bright. Those that responded readily were then assigned, at random, to one of four groups representing the possible combinations of the two reinforcing conditions and the original and the subsequent reversal learning tasks. Thus, some rats learned the original discrimination with food (F) reinforcement and learned the reversal task with ICS (S) reinforcement; while others received the combinations F-F, S-S, or S-F.

Each animal received 20 trials per day, with a 30-second interval between trials. If a correct response was made, a single 45-mg Noyes pellet or 0.5 second of intracranial stimulation was delivered. It should be noted that the response panels were adjusted so that the same degree of displacement was required for both food and stimulation reinforcement. Training continued until the performance criterion of 18 correct responses in 20 trials, the last 10 without error, was attained. The following day the animal started on the reversal task: the formerly positive stimulus now became the negative one, and vice versa. Training continued, as before, until the same criterion of discrimination was once again reached. Animals were then sacrificed and their brains removed for histological examination.

The results are summarized in Fig. 1. Each animal is represented by a line originating at his first-task score and terminating at his score on the reversal task. A line of positive slope thus indicates an animal that learned the second task less rapidly than the first. Examination of the figure suggests (and statistical analyses support) the conclusion that no systematic differences in first-task performance exist among the four groups. There is a tendency for the two groups that had intracranial stimulation as the first reinforcer (S-S and S-F) to be somewhat more homogeneous in first-task score than the other two groups, but this is probably a result of sampling error.

The focus of the experiment, however, is the training required by each 23 FEBRUARY 1962 animal to reach the performance criterion on the second task. If ICS reinforcement does indeed result in conditioning which is less permanent, more labile than conditioning accomplished with food reinforcement, a comparison of animals who are first conditioned with food and those first conditioned with intracranial stimulation should show the former to be more resistant to change and therefore slower to learn the reversal problem. The present results (Fig. 1) suggest quite the opposite conclusion: it is the animals that received ICS reinforcement on the first task that are both slower to reverse and poorer in performance than those that were first trained with food. Statistical analyses support these observations: Groups S-S and S-F contain the animals slowest to learn the second task (Mann-Whitney U = 48.5, p = .002, two tails); and the same groups contain the animals whose change in performance from the first to the second problem indicated the greatest degree of difficulty in handling the reversal situation (U =60.5, p = .01, two tails). Thus, in both an absolute and a relative sense it seems fair to say that the ICS reinforcement procedure resulted in performance which was more resistant to change than that produced by food reinforcement.

These results suggest there is nothing inherently impermanent about responses conditioned with ICS reinforcement, and that they may well be even more persisting than food-reinforced responses which have been carried to the same level of original response strength. No doubt the parameters of both the food and intracranial stimulation are important in determining these

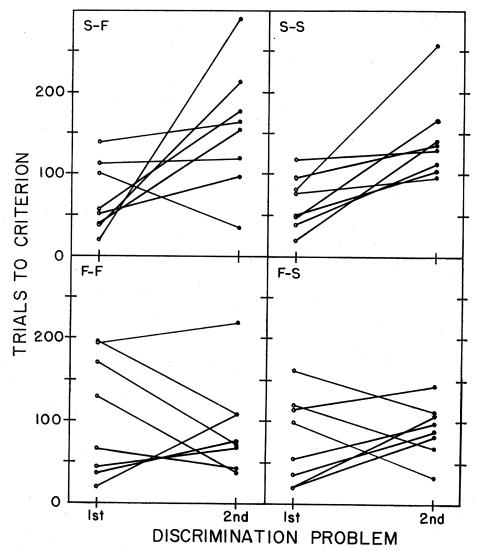


Fig. 1. Trials to learn the first discrimination and the subsequent stimulus reversal problem. Each line connects the scores of an individual animal. Reinforcing stimuli employed are indicated by F (food pellet) and S (ICS).

results: the values chosen in the present study were merely those which gave roughly comparable responding in a free-operant situation, but they did seem to yield reasonably similar performances on the first discrimination. It is also possible that the site of intracranial stimulation would influence the relative permanence of conditioning, but this remains a problem for future research. Finally, the results suggest that persistence of responding in reversed-discrimination situations may be a useful index of efficacy of reinforcement, since it appears to be sensitive to differences in reinforcement and at least partially independent of two of the more frequently employed measures, response rate and error elimination in original learning (7).

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Semantics in Biothermal Studies

Abstract. Only by the use of accurate and meaningful words pertaining to body temperatures and heat sources can our understanding of the ecological and physiological functioning of vertebrate organisms be clarified. Since the classical terms are inadequate, other terms that are already in use should be used.

The use of more appropriately descriptive terms in classifying thermal types among the vertebrates was originally proposed in 1940 (1) and explicitly reanalyzed and emphasized in 1947 (2). Since that time there has been an increasingly widespread acceptance of ectotherm in place of poikilotherm, and endotherm in place of homoiotherm. Less widely adopted have been heliotherm for those vertebrates that rely on periodic basking for their thermoregulation, and thigmotherm for those organisms that derive their effective body temperatures solely from the medium in which they live, water or soil. The latter have little or no capacity for thermoregulation other than by micro or macro migratory avoidance excessive environmental thermal of changes. Examples of thigmothermic vertebrates are fish; completely aquatic amphibian larvae and adults; marine turtles and sea snakes, though these may "bask" or at least float with parts of the body exposed to sunlight; burrowing snakes and lizards; and strictly nocturnal though surface-feeding amphibians and reptiles. All of these are primarily, at least, thigmothermic ectotherm organisms.

An occasional but increasingly encountered and confusing misuse of precise nomenclature is the substitution of the word heterotherm for ectotherm or poikilotherm as though it were equivalent. With increasing evidence for, and without evidence to the contrary, it can be presumed from all available information that most if not all terrestrial and marine vertebrates have specific thermal preferences or optima nearly as precise as those that characterize some of the endotherms. They appear to differ from the endotherms chiefly by their thermal plasticity when avoidance of unfavorable temperatures is impossible. If or when vertebrate animals are found that have no optimum and therefore flourish equally well throughout a wide range of temperatures, they should be called *eurytherms*, but they will nonetheless be ectotherms.

The term heterotherm should be retained in its original sense, that is, for those organisms which for some presently unknown reason or reasons are incapable of relying solely on either metabolic or external sources of heat under even moderately varying environmental temperatures. Employed in this manner, examples of heterotherms include at least some of the hummingbirds, some swifts, the western poorwill, probably the speckled coly (Colius striatus of Africa), and many nearctic bats. Heterotherm is the appropriate designation for these ambivalent compromisers between ectothermism and endothermism.

The ecologically semantic utility of these terms lies in the fact that each calls attention to the fundamental difference in sources of body heat. From the physiological-ecologist's point of view there is a vast difference in energy economics between ectotherms and endotherms. For example, in endothermic

organisms insulation conserves body heat and energy supplies, whereas it would effectively deprive ectotherms of most of their successful reliance on incoming radiant energy. In a similarly reversed manner the thermoregulatory function of an ectotherm's vascular system is primarily that of heat-uptake and distribution of this heat into the body, whereas in the endotherms the energy-expensive heat generated by metabolic processes in deeper tissues is carried outward to the surface where it may be lost. Recognition of these simple but fundamental differences immediately clarifies the functioning of attendant phenomena in a manner that is unattainable with the older nomenclature.

Insofar as comparative endocrinologists and physiologists become interested in the ectotherms it is abundantly clear to students of temperature that a much more pointedly descriptive nomenclature would be helpful, and might result in more useful studies than many of those that have been done in the past in these fields. So long as nonbiothermal specialists are beguiled by inaccurate thermal terms and therefore are led to think in the misleading older designations for thermal types, we can scarcely expect them to abandon the now nearly universal custom of conducting experimentation based on the resulting ambiguous assumption that for "poikilothermous" vertebrates room temperatures, or for that matter almost any nonlethal or nonextreme environmental temperature, will give meaningful, standard, and reproducible results.

From the vertebrate ecologist's approach, the source of heat and the regulation of body temperatures, involving as they do among other things, food and the energy balance, shelter, adaptations to climate, and the annual activity cycle, are certainly sufficiently important to justify the use of the most precise and descriptive terminology available. This insistence on accurate, verbally oriented thinking should be particularly true for those interested in any aspect of ectotherm research (3). **RAYMOND B.** COWLES

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