tions. A *t*-test of the difference between the difference scores (responses to the tone bar minus responses to the no-tone bar) before and after the pairings gave $t = 4.07$ ($p \simeq .001$, indicating a significant shift in lever preference. A *t*-test of the difference in response frequency at the tone bar before and after the pairings gave $t = 4.20$, $p \simeq .001$.

In contrast, neither of these effects was obtained in the brain shock neutral group. The preference for the no-tone bar, although diminished, persisted after the pairings procedure, and the absolute increase in response frequency at the tone bar was negligible.

It is concluded that electrical stimulation of septal and hypothalamic structures can serve as primary reinforcement in establishing secondary reinforcing powers in neutral stimuli. This finding does not seem to be consistent with a theory of secondary reinforcement which assumes that a neutral stimulus must be established as a discriminative stimulus in order to function as a secondary reinforcer (*10*).

It is tempting to speculate that what may be involved here is a kind of neural conditioning, with the tone serving as the conditioned stimulus and the brain shock as the unconditioned stimulus. After the pairings, the tone has reward value because it gives rise to a conditioned neural discharge of a reinforcing nature (in, presumably, the same structure, stimulated electrically). Indeed, it should be possible, through the use of brain-wave recording techniques, to determine directly whether neural activity produced by direct stimulation of subcortical structures can in fact be conditioned to a sensory input.

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7. Prior to the first day of training, all animals were placed in the chamber for 1 hour, during which time neither lever produced any tone, in order that original lever preference might be determined. The tone was then associated with the nonpreferred lever.
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9. In the case of several animals that had zero or near-zero rates in the first hour, additional test sessions were conducted to make sure that the placements were not positive.
10. W. N. Schoenfeld, J. J. Antonitis, P. J. Bersh, *J. Exptl. Psychol.* 40, 40 (1950). The operations that imparted secondary reinforcing properties to the tone in the study described in this report (that is, the pairings with brain shock) did not provide, at the same time, the conditions favorable to its development as a discriminative stimulus. This is because the effective delivery of the brain shock reward requires no (operant) response on the part of the animal, in contrast to conventional reward situations which involve approaching and consummatory behavior. In a case such as this, it is hard to see how particular responses could have been selectively reinforced with brain shock in the presence of the tone to permit the formation of a discrimination. Furthermore, the brevity of the interval between tone and brain shock (0.5 second) would make the development of superstitious behavior in response to the tone unlikely. No evidence of such behavior was indicated by observation.

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Effects of Brief Exposures to Cold on Performance and Food Intake

The relationship between food intake and temperature is usually studied, as is acclimatization in general, during prolonged exposure to one temperature. Under these conditions, rats typically show a configuration of changes that comprise the state called acclimatization. These include changes in heat production and food intake, endocrine structure and function, peripheral vascularization, and so on (*1*). In this paper, I report data (*2*) based on brief exposures to varied temperatures which appear to demonstrate acclimatization phenomena of very short latency.

Rats were exposed to a temperature of either 0°, 10°, or 20°C (±2°C) for 20 minutes per day. The apparatus used was a box 10 by 10 by 11 in. that contained a lever and a device for delivering a small pellet of food weighing about 0.04 g. The box was kept in an insulated enclosure connected to a refrigeration unit so that its internal temperature could be varied. The lever was connected in such a way that a food pellet was delivered once per minute, provided that the lever was pressed at the end of the period. This periodic reinforcement schedule was used in order to avert differences in food intake among the animals while they were in the apparatus. The animals were given access to food for only 1 hour following their exposure to the various temperatures.

Thirty male Sprague-Dawley rats, about 6 months old, were used as subjects. They were started on the study after 3 weeks of experience on the 1-minute periodic reinforcement schedule. Each animal was exposed to each temperature during each 3-day experimental period. There were eight of these periods, or 24 experimental days in all, for each rat. Three different sequences of exposure were used, with ten animals assigned to each sequence, and each group repeated its assigned sequence four times. These sequences were as follows: Group 1: 0°, 20°, 10°, 20°, 0°, 10°C; group 2: 10°, 0°, 20°, 10°, 20°, 0°C; group 3: 20°, 10°, 0° 0°, 10°, 20°C.

The performance criterion was the number of lever-presses made during each experimental session. The data on food intake are based on the amount of food eaten in the 1-hour period following the 20-minute exposure. This food was a commercial dog food (Red Chain) that had been crushed to powder form. Feeding cups with perforated inserts were used to prevent spilling.

Figure 1 shows the performance data for the first four periods (*3*). Each point in this figure is based on the performance of all 30 animals. During the first period, response frequency was greatest for the highest temperature and least for the lowest temperature. Then, because of increases in responses at the two lower temperatures, the frequency for all three temperatures became about the same. Since rats exposed to cold eat more food, one would expect them to respond more frequently at lower temperatures because of the correlation between length of food deprivation and rate of lever pressing (*4*).

Figure 2 reveals the amount eaten in

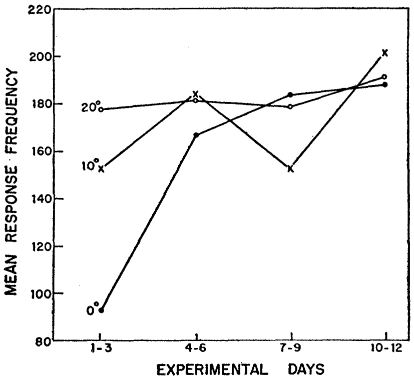

Fig. 1. Performance (lever-pressing) data at the three different temperature levels during the first four of the eight 3-day periods.

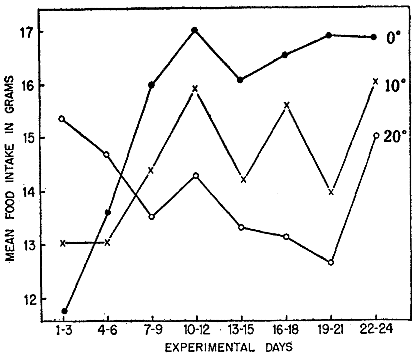

Fig. 2. Food intake during the hour that directly followed exposure to the three different temperatures to which the rats were subjected during the eight 3-day periods of the experiment.

the 1-hour period following exposure to the three temperatures during each of the eight 3-day periods. During the first period, the rankings are exactly the reverse of what would be expected on the basis of heat production and caloric need in the cold. By the third period, however, the rankings are in accord with this expectation. An analysis of variance performed on these data showed that differences among temperatures and periods attained the .001 level of significance.

A second study—this one of response to 20-minute exposures to temperatures of either − 10° or 20°C for six consecutive days—showed, during an 18-day period (which allowed for two reversals), results similar to those obtained in the first experiment. Both food intake and frequency of response at the lower temperature tended to increase for about 3 days and then to level off.

One criterion of acclimatization is a change in behavior that is more adaptive in one particular situation than in another. In the present situation, acclimatization would be evinced by a greater response frequency at lower than at higher temperatures (provided that bar-pressing is not inefficient as a method of producing and conserving heat for a limited period) and by an increase in the amount of food ingested after exposure. While the former did not occur, there was still a considerable rise in frequency of bar-pressing from the original level for the two lower temperatures, and I think it fair to call both the changes in bar-pressing behavior and in food consumption evidence of acclimatization—or, at least, a form of acclimatization.

The other feature of the data that seems pertinent to acclimatization is the retention of adaptation in the face of constant shuffling of the exposure temperature. Perhaps most striking is the specificity that soon appears in food intake. This short-term adaptation of energy intake to energy output is one of the three types of energy regulation postulated by A. Mayer (*5*), who, in the rabbit, found this short-term regulation to be the most precise of the three types. It must be emphasized once more, however, that the findings I am reporting are based on very brief exposures.

These data do not warrant making any statements about the ultimate mechanism of regulation of food intake. It would seem, though, that day-to-day regulation, at least with this feeding schedule, is quite sensitive to changes in temperature and that there is a short latency of response to its effects.

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2. These data were obtained in the laboratories of the Department of Experimental Psychology, U.S. Air Force School of Aviation Medicine. They were reported earlier at the 1957 meetings of the Federation of American Societies for Experimental Biology.
3. Only the first four periods are included in this graph because the animals were changed to a 3-minute periodic reinforcement schedule, beginning with the fifth period, and the data for the last four periods are therefore confounded with the response to the changed program.
4. B. F. Skinner, *The Behavior of Organisms* (Appleton-Century-Crofts, New York, 1938).
5. This work has been reviewed by J. Mayer [*Ann. N.Y. Acad. Sci.* **63**, 15 (1955)].

17 October 1957

Apparent Exception to the "All or None" Law in Cardiac Muscle

The "all or none" law as applied to muscle states that the strength of the contraction is independent of the strength of the stimulus. Recently my coworkers and I observed an apparent contradiction to this principle. We were repetitively stimulating, at threshold voltage, an excised cat papillary muscle in a saline (*1*) bath by means of mass platinum electrodes lying alongside the muscle. When the stimulus voltage was suddenly doubled, the contractions, after a few seconds' delay, became gradually more forceful until they were about 100 percent above the previous level (Fig. 1*A*). When the voltage was returned to the threshold value, the contractions, after some delay, returned to the base line. The phenomenon was repeatable, and all cat papillary muscles (18 in all) have shown this response in varying degrees. With a tenfold increase in stimulus voltage, the augmentation was much more pronounced.

These observations suggested that some fibers, quiescent at the lower voltages, were activated by the stronger stimulation—that is, that the papillary muscle was not a functional syncytium. The delay in the onset of the augmentation could be explained by assuming that some time was required before the recruited fibers reached maximum tension (treppe phenomenon). To test this suggestion the muscle was speared with a KCl-filled glass microelectrode having a maximum diameter at the tip of 0.5 μ (*2*). Resting and action potentials were recorded from 697 individual cells in 12 cat papillary muscles during electrical stimulation at threshold voltages (*3*). No cells were found that showed a resting potential but no action potential, such as might be expected to exist if the nonsyncytial hypothesis were correct. Accordingly, it was abandoned.

Results from eight isolated strips of cat atria suggested another hypothesis. In this tissue, under similar conditions, strong stimulation produced an initial depression, then a post-high-voltage rise in the contraction strength (Fig. 1*B*). Since acetylcholine would be expected to depress the contractions and would be expected to be present in the atria, it seemed possible that the strong stimulation had caused the release of this autonomic mediator. Indeed, atropine consistently blocked the depression and unmasked the augmentation produced by strong stimulation (Fig. 1*C*). These observations were consistent with the view that, in the atrium, both acetylcholine and a potentiating substance were released by the high voltage. When the stronger stimulation was terminated, the release of both substances diminished (or ceased), but the rapid hydrolysis of the acetylcholine permitted the poststimulation augmentation by the potentiating substance. The possibility that acetylcholine is responsible for both depression and augmentation cannot be overlooked. [Burn (*4*) cites several examples of the potentiation of contractions by low doses of acetylcholine.] If this were the case, however, one would expect that some augmentation would precede the depression, but this did not occur.

Since it seemed reasonably certain that acetylcholine was the depressing agent, it followed that epinephrine or norepinephrine might be the potentiating substance in both the atria and the papillary muscle. In addition to these considerations and the fact that these hormones are known to be present in heart muscle (*5*), there were other indications that implicated the epinephrines. For instance, spontaneous activity commonly

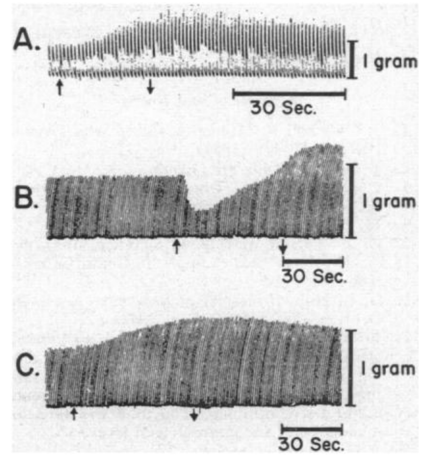

Fig. 1. *A*, Isometric contractions of driven papillary muscle of cat. At upright arrow, stimulus voltage was suddenly increased from 40 to 80 v; at inverted arrow, voltage was reduced to 40 v (threshold). *B*, Isometric contractions of left atrium of cat; arrows same as *A*. *C*, Same as *B*, 5 minutes after the addition of 10 μg of atropine to 8 ml bath.