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Heat sensitivity of the rat: heart rate conditioning with a thermal CS

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HEAT SENSITIVITY OF THE RAT: HEART RATE CONDITIONING WITH A THERMAL CS.

by

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ABSTRACT

Heat Sensitivity of the Rat: Heart Rate Conditioning with a Thermal CS.

Recent theoretical interpretations of the cutaneous sensory code may be categorized into non-specific temporal - spatial patterning explanations vs specific modality receptor mechanisms. Electrophysiological data based upon neurological responses of lower mammals to both mechanical and thermal stimulation support both positions.

Neurons sensitive to warming stimuli have been reported in the cat and parallel sensitivity to thermal stimulation has been demonstrated in behavioral studies with this species. Very few neurons sensitive to warming stimulation have been found electrophysiologically in the rat, and in addition, few experiments exist to indicate the ability of the intact animal to respond to this form of stimulation.

A radiant heat source was therefore used as the conditioning stimulus in a classical conditioning paradigm where changes in rat heart rate were treated as the conditioned response. In addition, noxious skin temperatures were investigated through the use of an escape response.

It was found that an infra-red radiation exposure calcalated to increase the rats' nose temperature 8.90°C did not produce a significant degree of heart rate change although a control group of animals established CRs to a light stimulus presented under similar conditions. Temperature increases

of 16.1°C were found to evoke escape responses; similar temperatures are noxious to both cat and human.

These results suggest that the rat is insensitive to local cutaneous temperature increases to which the dog, cat and human have demonstrated sensitivity. The data provide correlative support for the negative results of the electrophysiological studies with the rat. The rat may therefore be an improper experimental species for investigation of the problem of neural coding of the cutaneous warmth modality.

INTRODUCTION

Cutaneous sensitivity has a long history of investigation in both physiology and psychology. A recent review of this topic (Melzack & Wall, 1962) has attempted to define the areas of agreement and disagreement among workers in the field. One area of controversy concerns the nature of the signal system which provides information concerning stimulation of the skin to the central nervous system.

The specificity theory of cutaneous sensibility developed by von Frey at the end of the 19th century has been generally accepted. In this theoretical system the cutaneous sensory modalities of warmth, cold, touch and pain arise by stimulation of Ruffini end-organs, Krause end-bulbs, Meissner's corpuscles and free nerve endings respectively. Melzack and Wall (1962) suggest that this system rests upon three assumptions of specificity; anatomical, physiological, and psychological. The physiological assumption asserts that receptors are specialized to the extent that they respond most readily to a particular kind of stimulus energy, an assumption which has been generally accepted by modern investigators. The anatomical assumption however, lacks supportive data, for a correlation of sensation modality at particular spots with any single kind of anatomical structure apparently does not exist (Weddell & Miller, 1962). The psychological assumption suggests that stimulation of a receptor of a given physiological specificity results in a sensation particular to that modality,

regardless of the form of the stimulus energy. Thus, if pressure evokes neural activity in a pressure sensitive unit, sensations of pressure result. However, high levels of other stimuli to which the receptor is relatively insensitive may still initiate afferent activity. The specificity theory assumes that if the pressure sensitive receptor system is stimulated by thermal change, the sensation will not be one of warmth or cold, but again one of pressure. The phenomenon that cold objects feel heavier than neutral temperature objects is thus interpreted by suggesting that the inadequate stimulation of pressure sensitive afferents with a cold stimulus nevertheless results in a pressure sensation. (Zotterman, 1959).

Melzack and Wall, (1962) suggested that the psychological assumption is in error. Although a receptor may be most sensitive to a certain type of stimulation, this should not be interpreted to mean that only sensations appropriate to that type of stimulation will arise. A receptor may encode more than one form of stimulus energy by variations in the pattern of activity it produces, much as a telegrapher transmits information in a single wire through temporal variation in signal pattern. The psychological sensations which result will be appropriate to the form of either of the applied stimulus energies.

Electrophysiological Literature

The bulk of electrophysiological data comes from the

hairy bodies of lower mammalian species, and these data have revealed that neuronal activity in a single afferent neuron may be evoked by both pressure and thermal stimuli. The problem of interpretation arises when the experimenter attempts to define the nature of the sensation such activity might represent. As examples of such responses, Hensel and Zotterman (1951) reported that "touch" fibers in their cats were activated at temperatures below 25°C, and responded with brief phasic bursts of activity without a steady response rate to suggest skin temperature. Siminoff (1965) also reported afferent fibers in the cat skin which responded to both pressure and thermal stimuli. Thermal sensitivity again was low, for activity was evoked only at physiologically severe temperatures of 15°C or 45°C. Wall (1960) has suggested that the hairy skin of animals is to be expected to have neurons responding to two kinds of stimulation, for the fur provides insulation against small temperature changes, and extreme sensitivity to temperature is thus of minor importance to the organism.

On the other hand, Boman (1958) found many fibers sensitive only to mild cooling in the rat, cat and dog, although no fibers sensitive to warming were found in the infraorbital branch of the trigeminal nerve. Hensel, Iggo & Witt (1960) observed small type "C" afferent fibers in the cat leg which responded with great sensitivity to thermal stimuli alone. Units responding to temperature as well as pressure were also

reported. Hensel et al (1960) suggested that the difficulty of finding "C" fiber activity among larger fibers may account for the small number of similar findings.

In 1960, Iriuchijima and Zotterman observed small thermally sensitive fibers in the infraorbital branch of the trigeminal nerve, both in the dog and the cat. Some of these unmyelinated "C" fibers responded to small increases in temperature, the majority of them, however, were specific to cooling stimuli. In contrast to the "Aδ" fibers previously reported (Zotterman, 1959), these new units were not activated by tactile stimulation. In the rats studied, eleven "C" fibers from the saphenous nerve innervating the hind leg were found to respond specifically to cooling. Only three neurons were found which responded to moderate levels of warming. Some "C" fibers reported were thermally sensitive with thresholds at 41 to 43°C, much higher than thresholds usually associated with thermal sensitivity (Iriuchijima & Zotterman, 1960). Hensel, (1963) further reported "C" size fibers from the saphenous nerve of the cat which were sensitive to warming and cooling, and has reported fibers in the cat infraorbital nerve which were sensitive to warming of the nose area (Hensel, 1968). It was not established whether or not these neurons were myelinated.

The sensitivity of the "C" fibers reported by Hensel et al, (1960), Hensel, (1963) and Iriuchijima & Zotterman, (1960), is comparable to that reported in the cat tongue by

Zotterman, (1959), where temperature changes of less than 1°C evoked regular changes in spike rate. These tongue fibers were thought to be of the small myelinated "Aδ" class. Whole nerve recordings from the chorda tympani branch of the 7th cranial nerve innervating the dog tongue also suggested small sensitive fibers responsive to warming in this species. Thermal responses from the tongue of the rat and cat have also been reported (Makous, Nord, Oakley & Pfaffman, 1963; Pfaffman, 1961). Specific warm fibers were reported in the cat, and the studies with the rat found chemically sensitive cells which responded to cooling and warming. Responses to warming, however, were typified by a cessation of firing rather than a more positive response.

The experimental literature thus demonstrates the existence of afferent neurons which respond to thermal changes of less than 1°C in cutaneous temperature. Some of these fibers appear physiologically specific to temperature, failing to respond to other stimulation modalities within physiologically normal intensities. Others apparently respond to thermal, mechanical pressure and even gustatory stimuli in the tongue. The fiber type of many temperature and temperature-pressure sensitive neurons was not reported. The majority of thermally sensitive cutaneous fibers found respond to cooling; the literature contains fewer reports of neurons which respond to increases in temperature with increases in firing frequency. Reports of neurons in the rat

which respond to small increases in temperature are particularly scarce.

A large proportion of these data appeared in the literature after or concurrently with Melzack and Wall's (1962) review and were not included in their discussion. The existence of the temperature sensitive neurons may limit the need to propose a patterning theory in the peripheral system, since these fibers appear to be specifically receptive to thermal stimuli and could provide temperature information to the central nervous system. This is not to suggest that patterning might not play a role within the CNS, for the majority of activity reported in the dorsal horn cells of the classical spinal pathway for temperature apparently results from the synaptic junction of many types of afferents on these cells, at least in the cat. These dorsal horn cells therefore appear highly non-specific in character, and ascending information may be best explained with a pattern code hypothesis (Wall, 1960). Uttal and Krissoff (1966) point out that there is no reason to expect that the nature of the sensory code will be similar from level to level in the nervous system.

Behavioral Literature

The presence of neurological responses to stimuli does not in itself indicate that the organism is behaviorally responsive to these stimuli. A search of the experimental

literature reveals few studies which have investigated the ability of animals to make discriminations based upon temperature although such studies would provide greater insight into the nature of the modality. Since the neurons responsive to both pressure and temperature generally have low sensitivity to thermal stimulation, behavioral studies indicating high temperature sensitivity would support arguments for the functional significance of the "C" fibers reported above.

Downer and Zubek (1954) reported that the smallest discrimination that their rats could learn was a 10°C difference. Their stimulus situation was one in which the animals were negatively reinforced for choosing the warmer of two sides of a copper plate that formed the floor of the apparatus. The positive reinforcement side of the floor was at room temperature, reported at 25°C, while the negative side was heated to 35,45 or 55°C, providing discriminations of 10, 20 and 30°C. The authors found no difference in error scores to criterion after decortication of somatic areas I and II or frontal-occipital cortex. The striking feature of their data, however, is that error scores did not decrease in the preoperative animals as the temperature of the negative plate was increased. The 10°C discrimination group made a mean of 5.5 (S.D.=5.4) errors while the second group made a mean of 7.43 errors (S.D.=8.86) for a 30°C difference followed by 9.21 errors (S.D.=9.71) for a subsequent 20°C difference.

(Means and standard deviations computed from their data.) A possible interpretation of these results is that the animals were getting little information from the warm or even hot side of the apparatus. It seems more likely that the positively reinforced 25°C side of the copper floor in effect functioned as a heat sink, resulting in a cooling of whatever receptive area the animals utilized. Were this the case, the data indicate a discrimination between the adaptation temperature of the skin and cooling by a 25°C stimulus rather than the 10°C temperature discrimination reported. The data further suggest that differences of as much as 20°C on the warm side (35 to 55°C) had little effect.

An early study by Yoakum (1909) had similar results. A runway discrimination of 40° vs. 24°C was reported learned. Again, the discrimination would be possible on the basis of cooling sensations only.

Unfortunately these studies and that of Hardy, Stoll, Cunningham, Benson, & Greene, (1957) are the only behavioral studies where cutaneous temperature sensitivity has been investigated in the rat, and the last of these involves responses to noxious levels of stimulation exclusively.

Studies with the dog and cat have revealed greater sensitivity. Kenshalo, Duncan & Weymark (1967) obtained conditioned responses to increases in the cat's nose temperature of 1°C. When the radiant heat source stimulation area was enlarged to include the full face, the threshold was lowered

to 0.2°C. Whether or not full face stimulation allowed radiation to reach the subject's cornea is not clear. Dawson (1963) reported specific fiber activity to warming stimuli in the cat cornea. Increases in neural activity were reported for temperature increases as small as 0.058°C. The function of the thermally sensitive neurons in the hairy skin of these animals remains unknown, for Kenshalo et al (1967) were unable to obtain conditioned responses to mild degrees of warming or cooling of the inner thigh or footpad.

Thermal threshold data for the dog nose was collected by Murgatroyd, Keller & Hardy (1958). The animals could respond to radiation intensities as low as 0.0016 cal/sec/cm^2. Since the duration of the exposure was controlled by the animal, changes in skin temperature are unknown. The authors reported that this intensity is comparable to human facial thresholds at moderate exposure times. The sensitivity of other body areas of the dog was not investigated.

Behavioral sensitivity has thus been demonstrated for the cat and dog when exposed to thermal stimuli, and the thresholds found are similar to the thresholds for neural activity reported in the electrophysiological literature. Little data however exist to suggest either neural or behavioral sensitivity to warming stimuli in the laboratory rat. Perhaps some meaning can be obtained from a comparative view of these experimental species. Dogs and cats, as do all higher mammals, have skin glands which are capable of pro-

ducing some sweat, thus aiding in regulation of body temperature in warm ambient temperatures. Rodents, however, are poor temperature regulators in the heat, and have no such glands. Some regulation is achieved by licking the fur for evaporative cooling and additional body heat is lost through increases in respiratory rates (Hainsworth & Stricker, 1968; Prosser & Brown, 1961). Whether or not this behavior is initiated by cutaneous senses or hypothalamic temperature receptors in unknown, and behavioral studies at extreme temperatures do not provide a definitive answer.

It has been well demonstrated that rats in a cold environment will bar press to receive heat. Weiss and Laties (1961) found that rats would maintain a very narrow range of body and cutaneous temperatures by behavioral regulation of the duration and intensity of a large radiant heat source. Satinoff (1964) found that cooling the anterior hypothalamus and preoptic area inhibited the animals' responses for heat reinforcement, as cooling the brain tissue resulted in autonomic increases in body temperature, largely through shivering. Carlisle (1966a) found that warming the rat's hypothalamus inhibited responding for heat in a cold environment although subcutaneous temperatures fell to 29.8°C. Similarly, Murgatroyd and Hardy (1968) found that rats in a warm environment stopped working for cooling reinforcement when the hypothalamus was cooled, although skin temperatures remained high. The latter two results suggest that cutaneous tempera-

tures contribute little to behavioral responding in such situations, although Carlisle (1966b) suggested that behavioral responses began before central temperatures changed, indicating that peripheral information was probably important.

The preceding discussion illustrates that neuronal or behavioral sensitivity of the rat to increases in cutaneous temperature has received scanty attention. Negative results in the electrophysiological experiments (Boman, 1958; Makous et al, 1963; Pfaffman et al, 1961) and the ambiguous results of the behavioral experiments (Carlisle, 1966a, 1966b; Downer & Zubek, 1954) contrast with the behavioral and neuronal temperature sensitivity reported in the cat and dog (Hensel, 1968; Kenshalo et al, 1967; Murgatroyd et al, 1958).

Demonstrated behavioral sensitivity of the rat to thermal stimulation would suggest that temperature sensitive neurons remain to be found by the electrophysiologist, while a lack of sensitivity suggests that such afferents may not be common in this species. It is the purpose of this study to investigate the sensitivity of the rat to temperature by using increases in skin temperature as the conditioning stimulus in a classical heart rate conditioning experiment. In addition, in order to eliminate the possibility that pain is the conditioning stimulus, the pain temperature threshold is estimated using an escape learning procedure. Although thermal pain has been reported for the cat at 53°C, (Rice & Kenshalo, 1962) and 52 - 53°C for the rat's back, (Hardy et

al, 1957) apparently no data exist for the rat nose and face, the area stimulated in this study.

METHOD

Two experiments were conducted. Experiment I determined escape latencies during exposure to thermal radiation at three intensity levels. Experiment II investigated the sensitivity of the rat to warming radiation by using changes in S's heart rate as a response measure in a classical conditioning paradigm. The latter experiment used three different conditioning stimuli. In a pretraining situation, Condition C, a click CS was used. In Condition H, the experimental group, the CS was exposure to an infra-red heat source of less intensity and duration than used in Experiment I. In Condition L, the control group, the CS was a light that gradually increased in brightness during the CS-UCS interval. One purpose of the control stimulus was to demonstrate that the transfer of training from the pretraining stimulus to a second stimulus modality did not inhibit responding to the second CS. In addition, the gradual onset of the light CS controlled for the gradual change in skin temperature during the CS-UCS interval with the thermal CS.

In view of the fact that conditioning per se was not of central interest in this study, the usual habituation and pseudoconditioning control groups were not used. The purpose of such groups is to separate responses made to the CS alone from those resulting from the associative relationship of CS and UCS in the conditioning group. In this study however,

the focus was on responses to the conditioning stimuli. Whether these responses occurred as a result of "true" associative conditioning (Rescorla, 1967) or some other process was not under investigation.

Subjects

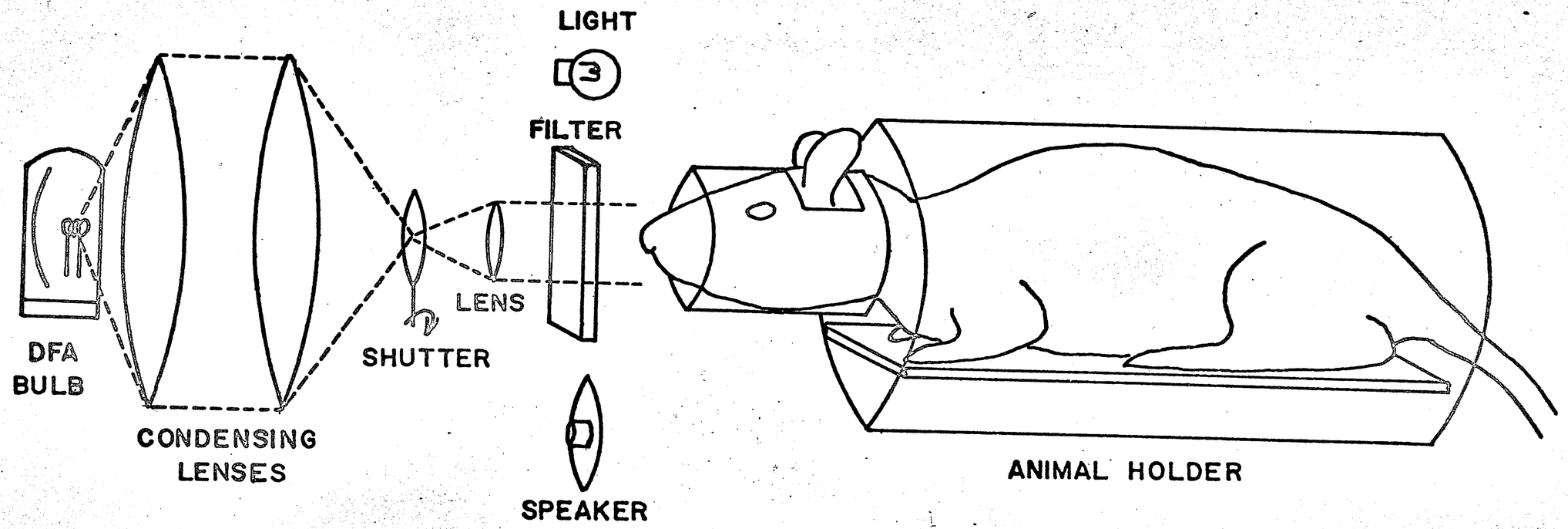
Thirteen naive female albino rats were used as Ss. Five Ss were used in Experiment I. Ten animals, including two which were studied in Experiment I, were used in Experiment II. After pretraining the latter animals. (Condition C) five Ss were exposed to the heat CS (Condition H) and five to the light CS, (Condition L).

Apparatus

Animal holder. The animals were held (Figure 1) in a plastic cylinder with a small section at one end into which the head would just fit. This holder is similar to the one available from A. H. Thomas Co., Philadelphia, Pa. A cutout allowed the animals pinnae to protrude. During exposure to radiant heat, a funnel shaped headholder was used. This allowed little vertical or horizontal movement of the S's head, and held the nose area in a relatively constant position. In addition, this piece shielded the S's eyes from light from the heat source. The headholder used during Condition L was transparent.

Radiant heat source. Light from a 150 watt Sylvania

Figure 1. Schematic diagram of the apparatus. Not shown is a large shield which prevented visible light from reaching the animal. The heat source, light and speaker were enclosed in a box about 4 x 5 x 12 inches in size.



SCHEMATIC OF THE APPARATUS

FIG. 1

DFA projector bulb was gathered by a double convex condenser lens system and focused at a shutter used to control the duration of the stimulation of the animal. A 19 mm lens was used to deliver a collimated beam of radiation to the animal when the shutter was open. This beam had a cross section area of 3.6 cm^2. The shutter itself was a disk of aluminum covered with asbestos sheeting and highly reflective aluminum foil. A small permanent magnet attached to the shutter caused it to open and close when the current flow in two adjacent electromagnetic coils was reversed. Foam rubber stops limited the extent of shutter travel, and 70 db white noise was used to mask what little shutter noise remained. A Corning #2540 filter passing only infra-red radiation >850 mμ was placed over the final lens in order to prevent visible light from reaching the animal when the shutter was open. In addition, a large cardboard screen surrounded the front of the thermal stimulator to further prevent light from the rear of the system from reaching the animal. This radiant heat source was similar to that described by Kenshalo et al (1967).

Radiant energy from the stimulator was measured with a calibrated thermopile, (Eppley #6440) placed at the position of the S's nose. Recalibration was periodically done to control for variation in the source. Energy output of the stimulator was controlled by varying the voltage applied to the filament. This voltage was monitored with a Ballantine

Laboratories Inc. Model 300 AC precision voltmeter and adjusted with a W2MT Variac transformer.

Radiant energy - skin temperature relationship. A relationship between skin temperature and duration of exposure to radiant energy has been developed by Hardy et al, (1957) and may be expressed as

$$\Delta T_s = \frac{2Qr\sqrt{t}}{\sqrt{\pi\ kpc}}$$

where ΔT_s is change in skin temperature in °C, Q = cal/sec/cm^2 of applied heat, r is absorbing power of the skin, k is heat conductivity in cal/sec/cm/°C, p is skin density in g/cm^3, c is specific heat in cal/g/°C, and t is exposure time in seconds. The product kpc, thermal inertia of the skin, has been found to be 84×10^{-5} $cal^2/cm^4/°C^2/sec.$ for depilated rat skin, (Hardy et al, 1957). A source of known Q value defines the relationship between stimulus duration and skin temperature. The relationships for the Q values used in the present experiments are shown in Figure 2.

Skin temperature measurement. A copper - stainless steel thermocouple contained in 1 mm diameter glass tubing was used to measure the normal skin temperature of one S's nose. This thermocouple was calibrated in water of known temperature and was found to have a sensitivity of 3.25 μ-volts/°C within the temperature range used.

Condition C, pretraining, CS. The click conditioning stimulus used in pretraining was a 13/second train of DC

Figure 2. Time course of the stimuli.

Q 1 to Q 4 show increases in skin temperature as a function of radiation intensity and exposure duration estimated according to the formula of Hardy et al (1957). The data points on Q 2, Q 3, and Q 4 show the escape response latencies and final skin temperatures obtained in Experiment I. Q 1 is the radiation level used as the heat conditioning stimulus in Experiment II. The broken line shows the increase in voltage (right ordinate) across the light CS (Condition L). Final illuminance was 8.9 footcandles at the S's eye. (See text for further details).

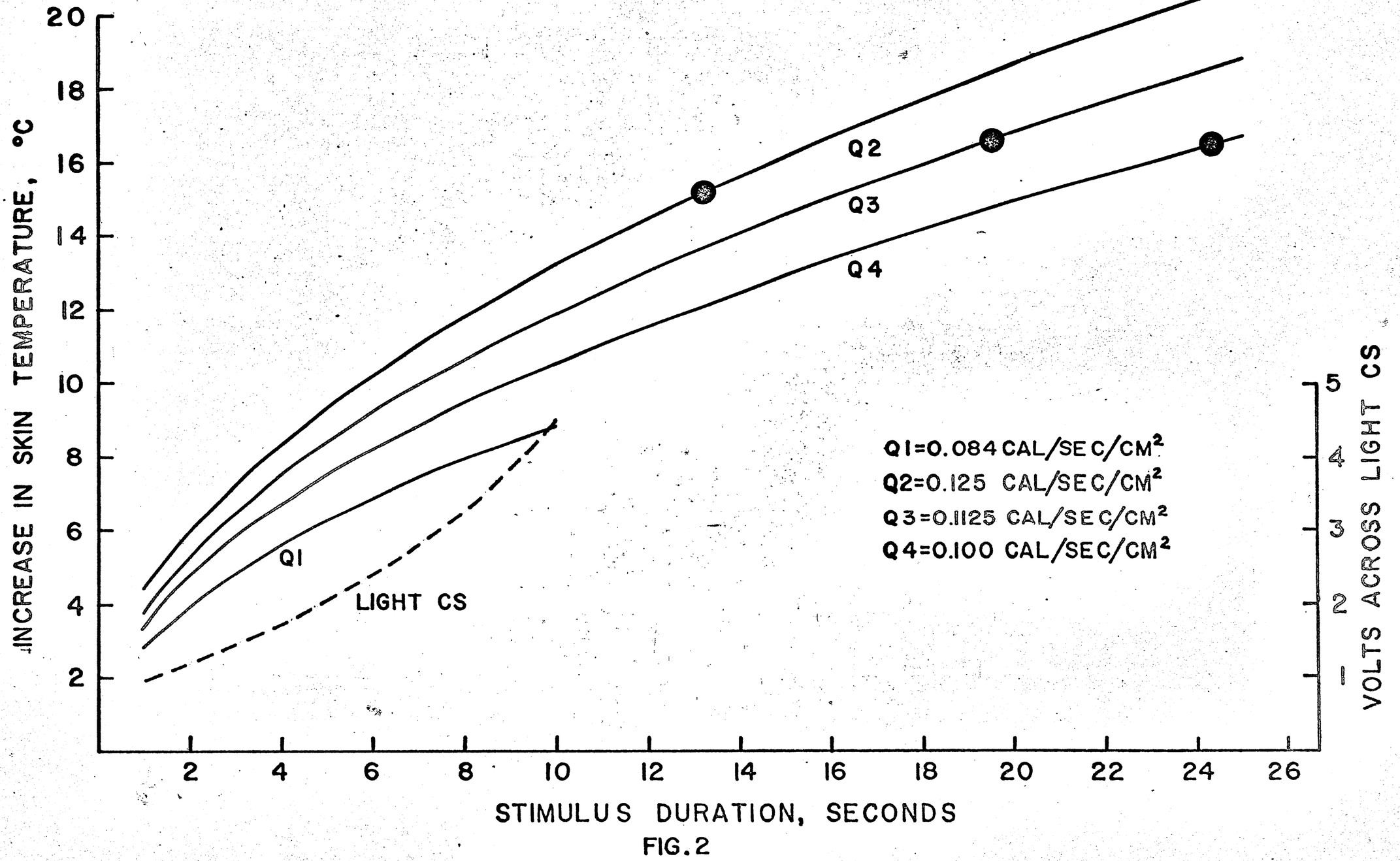

INCREASE IN SKIN TEMPERATURE, °C
VOLTS ACROSS LIGHT CS
STIMULUS DURATION, SECONDS
Q1
Q2
Q3
Q4
LIGHT CS
Q1=0.084 CAL/SEC/CM²
Q2=0.125 CAL/SEC/CM²
Q3=0.1125 CAL/SEC/CM²
Q4=0.100 CAL/SEC/CM²

FIG. 2

pulses applied to the speaker mounted in the thermal stimulator. The sound level was adjusted to about 70 db at the position of the animal's head.

Condition L, light CS. The conditioning stimulus for the control group was a small GE #63 6 volt bulb. A synchronous motor was used to turn a potentiometer in series with the bulb filament, thus providing a gradual increase in voltage to the bulb. The time course of this stimulus can be seen in Figure 2, where the right ordinate indicates voltage applied to the bulb. Maximum illuminance was equal to 8.9 foot-candles at the position of S's eye.

Unconditioned stimulus. The unconditioned stimulus used in Experiment II was provided by an AC shock source giving a short circuit current of 0.45 ma. This was applied to the rat's tail through two 1/4" diameter EEG electrodes taped on opposite sides of the tail. Standard EEG recording paste was used to provide good contact.

Recording apparatus. The latency of the escape response in Experiment I was recorded on a Standard Electric S-1 timer reading in 1/100 second. A Grass model 7 polygraph with 7P5A preamplifier and 7DAC driver amplifiers was used to record S's heart rate in Experiment II, as well as provide CS and UCS signal marks on the same time base. Chart speed was 36 mm/sec. This polygraph was also used to record the voltage output of the thermocouple used to measure skin temperature.

Stimulus programming. The CS - UCS interval and presentation of the various stimuli used in Experiment II were controlled through the use of two Hunter 111C interval timers. CS duration was 10.5 seconds, the UCS occurred during the final 0.5 second.

All experimental sessions were conducted with the animal inside an Industrial Acoustics Co. Inc. Model 402A acoustic chamber so that extraneous noises would not reach the subject. Average ambient temperature in the chamber was 28°C.

Procedure

Normal skin temperature measurement. Since the conscious animals would not tolerate the pressure of the copper - stainless steel thermocouple against their noses, the nose surface temperature of a rat lightly anaesthesized with Nembutal was measured. Four measurements were made during the first twenty minutes of anaesthesia, prior to the time the temperature depressant effects of the drug occurred, for S's rectal temperature did not fall below 37.5°C.

Experiment I. Five animals were habituated to the animal holder for two hours. The thermal stimulation was then delivered by opening the shutter of the heat source and starting the recording timer simultaneously. When the animal attempted an escape response, (a clear withdrawal movement of the head as far as possible into the holder) E

stopped the timer and closed the shutter. The recorded latencies of the escape responses thus include E's reaction time.

Q values of 0.100, 0.1125, and 0.125 cal/sec/cm^2 were obtained by adjustment of the voltage to the radiant heat source. The time course of the increase in skin temperature estimated by the formula of Hardy et al (1957) for these radiation intensities is shown in Figure 2, (Q 2 - Q 4). Fifteen trials at three minute intertrial intervals were given, five trials at each of the three energy levels. These levels occurred in random order. Latency times for each energy level were then converted to increases in skin temperature according to the formula of Hardy et al (1957). Means and standard deviations were computed for each stimulus level.

Experiment II

Pretraining: Condition C. Ten Ss for the heart rate conditioning procedure were anaesthesized with ether. Two stainless steel wire loops used as recording electrodes were inserted subdermally, one dorso-medially just rostral to the scapulae, and one over the thorax just dorsal and caudal to the right foreleg. After a minimum of 24 hours recovery from this procedure, two hours habituation to the animal holder was given. On the following day, 25 click CS habituation trials were given to the Ss with a 60 second mean

intertrial interval (ITI), 30 to 90 second range. This procedure was followed by 25 conditioning trials, in which the last 0,5 second of the 10,5 second CS was paired with the 0.45 ma AC shock UCS. The mean ITI during conditioning was three minutes with a two to four minute range. Reinforcement was omitted on every fifth trial. On the second day of conditioning, the Ss underwent 25 additional trials with the same stimulus parameters. Of 14 animals tested under this procedure, 10 that gave reliable CRs were selected to continue in the experiment. The four animals rejected became extremely excited and active following presentation of the UCS, and no stable change in heart rate occurred during the CS - UCS interval within the 50 pretraining trials.

Radiant heat CS: Condition H. Five animals from the pretraining condition were assigned to the radiant heat CS group. These Ss received 25 CS habituation trials of 10 seconds duration. A three-minute mean ITI was used to allow recovery of normal nose temperature. Five conditioning sessions of 25 trials each were conducted on the next five days. The UCS parameters were similar to the pretraining condition. Voltage to the radiant heat source was adjusted to produce a Q value of 0.084 cal/sec/cm^2. According to the formula given above, (Hardy et al, 1957) skin temperature would rise 8.9°C during the 10 second CS - UCS interval used. This is shown in Figure 2, (Q 1.). The radiant energy was aimed directly at the the animal's nose. Following the

final heat CS conditioning session, a final session of conditioning with the click CS was given. (Recall session)

Light CS: Condition L. The five remaining animals from the pretraining condition were used in this group. Two of these animals had been Ss in Experiment I. The light CS was presented 25 times without reinforcement with a one minute mean ITI. Two successive days of 25 trials per day followed. All conditioning parameters were similar to those of the other two conditions. Although no shutter was used with the light CS, white noise was used as it was for the heat CS group. Except for the different CS, all conditions for the light and heat CS conditions were similar.

Heart rate measurement. The distance between the last 20 heartbeats prior to the CS onset was measured to the nearest 1/2 mm, and with the known recording chart speed of 36 mm/sec., this measurement was converted to beats per minute. (BPM) This measure was repeated for the last 20 beats prior to UCS onset at the end of the CS. Pilot data and examinations of the experimental results indicated that this 20 beat sample yielded the maximum change occuring in the interval. The difference between the two thus represents any change in heart rate during the delivery of the CS. Means for blocks of five trials were computed for each animal. A sample data record may be found in the Appendix, Figure 5.

RESULTS

The animals in general were quiet in the holder after the habituation period, and freely entered the apparatus at the beginning of the experimental session on succeeding days.

Experiment I

Temperatures computed from the latency data at which the animals attempted escape or withdrawal responses are shown in Table 1, where the data of Hardy et al (1957) are also presented. As can be seen, the escape temperature at each of the three radiation intensities is relatively constant. The points on Figure 2, where the exposure time - temperature increase functions are shown for the stimulus intensities, also indicate these data. Subtracting 1/2 second for E's reaction time from the latency of S's response would only reduce the temperature means by about 0.5°C. Figure 3 indicates the mean escape temperature of the five animals for each trial at the three intensity levels.

The nose temperature of the S under light Nembutal anaesthesia averaged 34.6°C. The overall mean temperature increase which produced escape responses was found by averaging the response temperatures from the three stimulus intensities used in this experiment. Adding this figure (16.1°C) to the 34.6°C initial nose temperature indicates

TABLE 1

Experiment I: Mean Escape Response Temperature Thresholds, Δ°C

Statistic	Intensity Level (Cal/Sec/Cm2)			
	0.100	0.1125	0.125	

Experiment I: Nose Stimulation

Mean Increase in Temperature	16.5	16.6	15.2	
Standard Deviation	± 1.8	± 1.8	± 2.1	

Statistic	Intensity Level (Cal/Sec/Cm^2)			
	0.120	0.144	0.186	0.231

Hardy et al, 1957: Back Stimulation

Mean Increase in Temperature	16.6	16.1	17.6	16.9
Standard Deviation	± 1.7	± 1.3	± 1.2	± 0.9

Figure 3.

Mean escape (noxious) temperature as a function of trials at the three radiation intensities in Experiment I. Each point represents the mean of five animals.

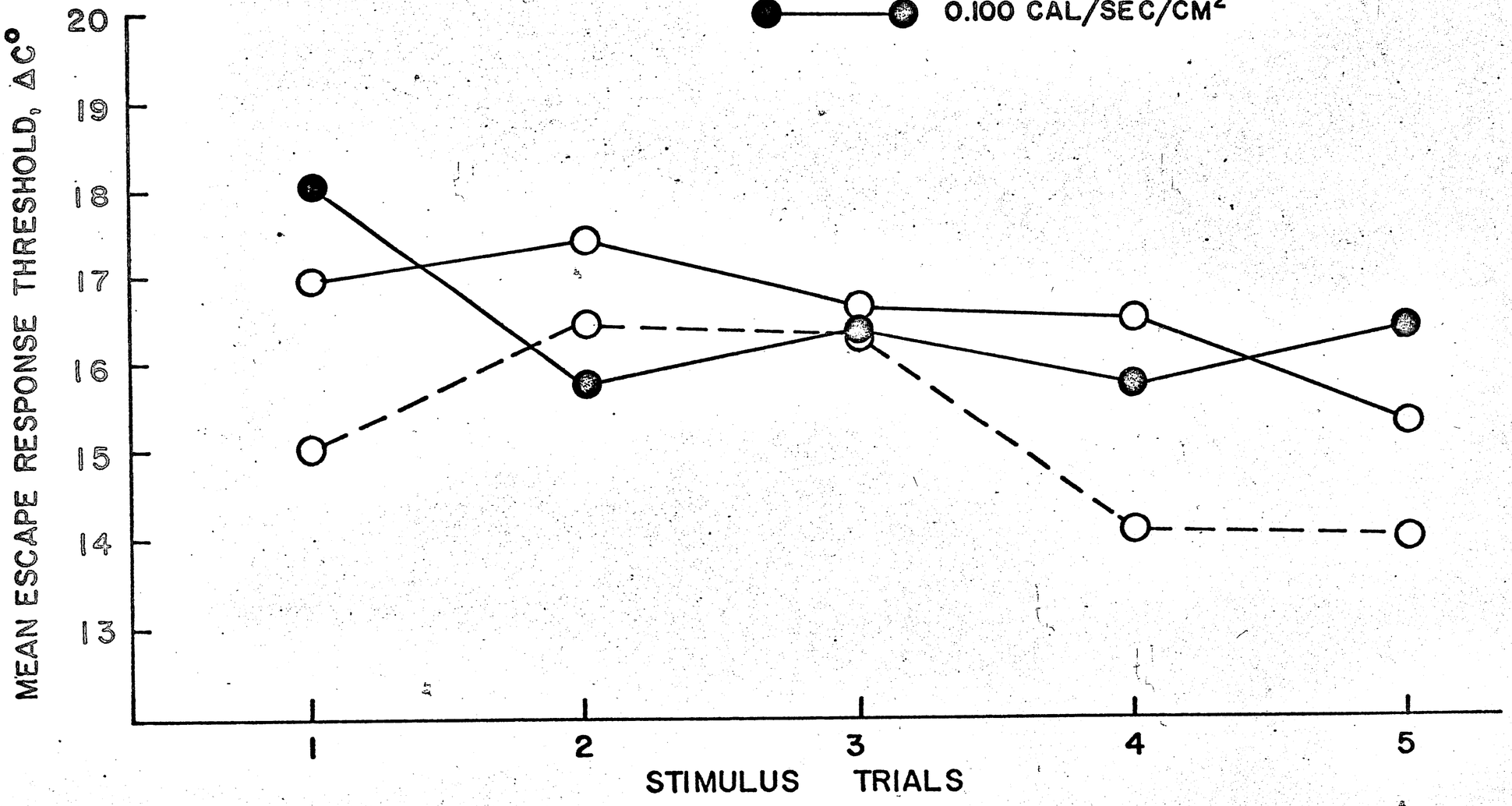

0.125 CAL/SEC/CM²
0.1125 CAL/SEC/CM²
0.100 CAL/SEC/CM²
MEAN ESCAPE RESPONSE THRESHOLD, ΔC°
20
19
18
17
16
15
14
13
1
2
3
4
5
STIMULUS TRIALS

FIG. 3

that the mean final temperature at which escape responses occurred was 50.7°C.

Experiment II

The results of the conditioning procedure are shown in Figure 4, where the sequence of conditions described above are indicated along the abscissa. The pretraining with the click CS, Condition C, shows an overall gradual increase in degree of heart rate deceleration to the CS during the first 25 trials. The second day of training resulted in large early session responses which decreased in magnitude during the session. Considering each of the five trial means as a treatment in a single factor, 15 treatment by 10 subject with repetitions design, (Winer, 1962; p. 105) a significant difference exists in the change of heart rate during the CS period. ($F=9.38$, $p.<.01$, Table 2.). On the final day of pretraining with the click CS, no significant difference existed between those animals later used in either Condition H or Condition L, either in mean response magnitude, ($t=1.33$) or variance, ($F=3.18$, Table 3).

No significant difference occurred as a result of the conditioning procedure with the radiant heat CS, ($F=1.14$) again in a single factor with repetitions analysis of variance, (Table 4). Significant changes in heart rate did occur in the group exposed to the gradual onset light CS, Condition L, in a similar analysis, ($F=7.96$, $p<.01$, Table 5).

Figure 4. Changes in heart rate (CRs) during the interstimulus interval: Experiment II. CC refers to the pre-training click CS, Condition C; CH the heat stimulus, Condition H; and CL the gradual onset light CS, Condition L. The numbers on the abscissa indicate the session day of successive exposure to each stimulus.

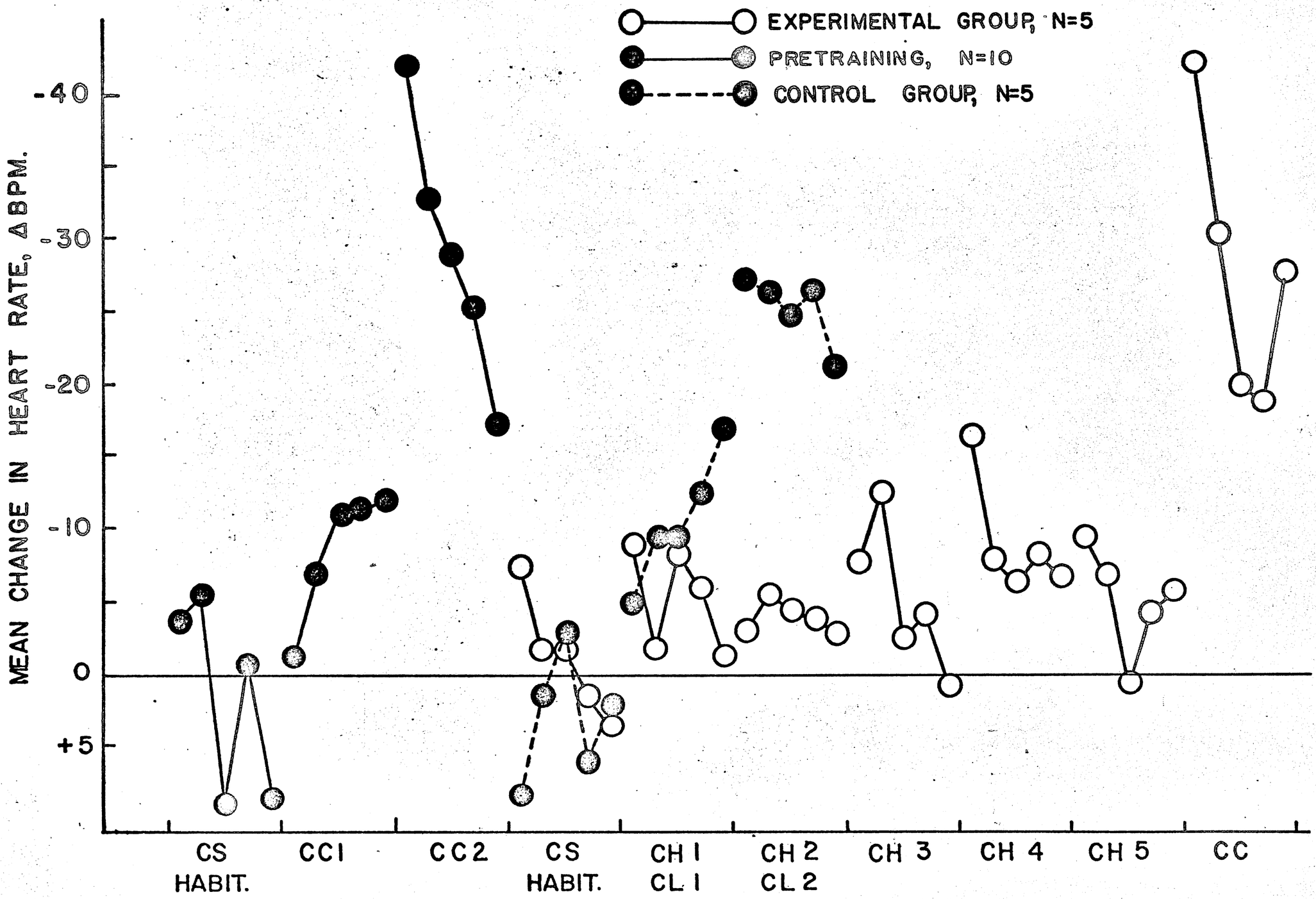

EXPERIMENTAL GROUP, N=5
PRETRAINING, N=10
CONTROL GROUP, N=5
MEAN CHANGE IN HEART RATE, ΔBPM.
-40
-30
-20
-10
0
+5
CS HABIT.
CC1
CC2
CS HABIT.
CH 1 CL 1
CH 2 CL 2
CH 3
CH 4
CH 5
CC

FIG. 4

TABLE 2

Analysis of Variance, Pretraining: Condition C

Source of Variation	df	MS	F
Between Subjects	9	736.14	
Five Trial Block Means	14	2345.28	9.38**
Residual	126	249.95	

**$F_{.99}(14,126) = 2.34$

Note: A constant = 60.0 was added to the raw scores to eliminate negative numbers (HR accelerations) and thus simplify the arithmetic of the analysis.

TABLE 3

t Test: Experiment II

Pretraining Subgroups: Condition C, Second Session

Statistic	Subgroups	
	Thermal CS; N=5	Light CS; N=5
Five Trial Block Means Δ BPM	47.24	36.24
	38.54	26.94
	32.49	23.01
	31.28	19.08
	13.89	20.54
Session Mean	32.71	25.16
Variance	150.28	47.22
Test	t=1.33, df=8	F (4,4) = 3.18
	$t_{.95}(8) = 2.31$	$F_{.95}(4,4) = 6.39$

TABLE 4

Analysis of Variance, Thermal CS: Condition H

Source of Variation	df	MS	F
Between Subjects	4	191.00	
Five Trial Block Means	29	86.59	1.14
Residual	116	76.02	

$F_{.95}(29,116) = 1.70$

Note. -- A constant = 20.0 was added to the raw scores to eliminate negative numbers (HR accelerations) and thus simplify the arithmetic of the analysis.

TABLE 5

Analysis of Variance, Light CS: Condition L

Source of Variation	df	MS	F
Between Subjects	4	418.81	
Five Trial Block Means	14	797.43	7.96**
Residual	56	100.20	

$**F_{.99}(14,56) = 2.66$

Note. -- A constant = 30.0 was added to the raw scores to eliminate negative numbers (HR accelerations) and thus simplify the arithmetic of the analysis.

In a comparison of the results of the second day of Condition L vs. the maximum heart rate changes occuring Condition H (4th conditioning day), a significant difference is found, $t=7.48$, $p<.01$, while variances of the two groups may be considered homogeneous, ($F=2.90$, Table 6). Finally, exposure of the Ss of Condition H to a final conditioning session of conditioning with the pretraining click CS yielded heart rate decelerations apparently equal to those found with these animals on the second day of pretraining condition C. ($t=1.01$, Table 7).

TABLE 6

t Test: Experiment II

Condition L (Session 2) vs Condition H (Session 4)

Statistic	Experimental Condition	
	Light CS; N = 5	Thermal CS; N = 5
Five Trial Block Means Δ BPM	27.10	16.33
	26.18	7.90
	24.76	6.26
	26.52	8.23
	21.06	6.67
Session Mean	25.12	9.08
Variance	5.90	17.11
Test	t = 7.68**, df = 8	F(4,4) = 2.90
	$^{**}t_{.99}(8) = 3.36$	$F_{.95}(4,4) = 6.39$

TABLE 7

t Test: Experiment II

Pretraining vs Condition C Recall. Condition H Subgroup.

Statistic	Experimental Condition		
	Pretraining, Session 2, N = 5	Condition C Recall, N = 5	Difference
Five Trial Block Means Δ BPM	47.24	42.14	5.10
	38.54	30.22	8.32
	32.49	19.87	12.62
	31.28	18.88	12.40
	13.89	27.71	-13.82
Means	32.68	27.76	4.92
Test	t = 1.01, df = 4		
	$t_{.95}(4) = 2.78$		

DISCUSSION

Experiment I

A clear response to the stimulus could be recorded when the animals made a sudden ~~jerk~~ in attempting to withdraw their heads to the rear of the headholder. The trial was then terminated as rapidly as possible. The calculated increase in skin temperature which evoked this response was 16.1°C averaged across all radiation intensities. Assuming that the initial skin temperature of all Ss was similar to the animal measured, (34.6°C) a final skin temperature of 50.7°C was estimated as the mean escape response temperature.

Were the rate of temperature change the relevant stimulus in this situation, the escape response temperatures would be expected to vary as the rate of skin temperature change is varied. The consistency of the escape response temperature across the three intensities of stimulation demonstrates that it was the temperature of the skin, not rate of temperature change, that controlled the S's behavior. Similar results were reported by Hardy et al (1957) for the rat's back, (Table 1).

The results summarized in Figure 3 indicated that in the small number of trials used, no major decrease in escape thresholds developed. Sensations occurring below the escape threshold were not utilized by the animals as cues for an

avoidance response. This is interesting in view of the report of Hardy et al (1957). In their paper, they reviewed previous data which indicated the existence of two distinct pain thresholds for intense thermal radiation in man. When stimulation occurred on the forehead, pain was reported at about 45°C. At about 54°C a "wince" or pain reaction threshold occurred. These temperatures compare favorably with the two response thresholds reported by Hardy et al when the rat's back was stimulated. At about 45.5°C a marked "twitching" of the rat skin was observed. At 51 - 52°C, the experimenters reported that the unrestrained animals attempted to escape from the experimental cage. It is not clear why the lower temperature "twitch" response was not used by the animals as an avoidance response cue to prevent continued stimulation. The problem would be difficult to investigate however, for an experiment involving repeated stimulation with high intensity radiation could cause tissue damage that would confound results. In the present study, because of the frequent spontaneous movement of the rats' noses, (sniffing, etc.) no consistent response which could be termed a skin "twitch" could be noted.

As mentioned above, Rice and Kenshalo (1962) found that the cat's back thermal pain threshold was 53°C. This represented a 16°C increase over the prestimulus skin temperature. Kenshalo et al (1967) reported that a final skin temperature of 48.8°C on the inner leg or 51.1°C on the footpad

was necessary before the experimental cats could successfully make an avoidance response. The latter two thresholds were constant regardless of adapting temperature. Kenshalo et al assumed a normal skin temperature of 35.5°C, therefore these latter figures represent increases of 13.3 and 15.6°C respectively. The proximity of these values to the thermal pain threshold found with the escape situation (Rice and Kenshalo, 1962) as well as the fact that humans report pain at these temperatures, (Teichner, 1957; Hardy et al, 1957) led Kenshalo et al (1967) to interpret their data as pain thresholds rather than responses made to a warming stimulus.

The higher noxious temperatures reported by all authors thus agree quite well for the cat's back and footpad, man's wrist and forehead, and rat's back and nose, all lying within a 50-54°C range.

Although pain thresholds are closely related to stimulus values producing tissue damage, regardless of stimulus modality, (Sweet, 1959) escape thresholds from animals of demonstrated thermal sensitivity of the nose, such as the cat, (Kenshalo et al, 1967) or the dog, (Murgatroyd et al, 1958) would certainly be of interest here. Low thermal pain thresholds from these animals might contrast meaningfully with the data from the rat's face, particularly in view of the insensitivity of the rat to warming stimuli reported in Experiment II.

Experiment II

Pretraining Condition C. In the design of this study, a major problem in choosing a response measure arose since the animal had to be strictly confined to permit localized stimulation with the thermal conditioning stimulus. The heart rate measure was selected for it did not require any skeletal movement on the animal's part, and the heart rate conditioning literature suggested that responses could usually be obtained in 10 to 15 CS - UCS pairings. (Black & Black, 1967; Fitzgerald, Vardaris, & Brown, 1966; Holdstock & Schwartzbaum, 1965.) However in pilot work before the present study, most Ss failed to acquire CRs to the clearly audible click CS during the first 25 trials. Conditions of this pilot work replicated the parameters used by Holdstock and Schwarzbaum, (1965) where CRs were obtained within one session. The early trials of the second day of pilot conditioning produced large responses however, even among those animals which previously gave only a few small heart rate decelerations during the CS period. The same effect appeared during pretraining Condition C. Responses on the first day were small in magnitude, but large during the early trials of the second pretraining day. These initial large responses which decreased in magnitude during the session appear similar to those obtained by Holdstock and Schwartzbaum, (1965) in the successive daily sessions of their experiment. It may by hypothesized that this decrease

was due to habituation to the UCS or perhaps depletion of transmitter substance at the vagus-heart junction. The magnitude of the responses obtained during the second session of pretraining or on the final day of conditioning with the click CS is similar to that reported by the other experimenters cited. Possible causes of the difference on the first day were not isolated but may be due to subject differences or inhibition produced by the confinement of the animal's head.

Heat CS: Condition H. The 0.084 cal/sec/cm^2 level of radiation used for the CS was calculated to cause an increase in skin temperature of 8.9°C during the CS - UCS interval. With a 34.6°C initial temperature, a final CS temperature of 43.5°C results. Assuming that a "twitch" or pain threshold exists at 45.5°C in the Ss of this experiment, as for those of Hardy et al (1957), it seems clear that the final CS temperature was below this "twitch" level, and well below the escape temperature (50.7°C) demonstrated in this experiment. The conditioning stimulus on the other hand is well within temperature levels which produce warming or heat sensations in the human, (36°C, Teichner, 1957) and far above temperatures producing conditioned responses in the cat, (Kenshalo et al, 1967) or the dog (Murgatroyd et al, 1958). Furthermore, the conditioning stimulus temperature was well above the 3.5°C CS used by Kenshalo et al (1967) as a pretraining stimulus in the cat. The general failure

of the rats in this study to respond to the CS of the experiment was therefore surprising considering the intensity of the stimulus, but comprehensible in view of the failure of electrophysiological workers to find neurons sensitive to warming stimuli in this species.

The interaction of the heart rate deceleration response and the form of the conditioning stimulus presents an interesting situation. During a training session, the S's heart rate showed spontaneous (non- CS or UCS related) accelerations and decelerations. It was difficult to define clearly whether or not a given CS presentation produced a conditioned response or merely a random change. Averages over trials or across subjects are needed to make any CS control apparent at low response levels of conditioning. In addition, the relatively long latency of the beginning of a conditioned deceleration (about one second) suggests that a short CS - UCS interval would produce small heart rate changes, even though the CS is clearly supra - threshold. In the present experiment, the gradual warming of the skin with the thermal CS in effect shortens the interstimulus interval, assuming that the absolute threshold is exceeded during the programmed CS "on" period. This effect, in conjunction with the long latency and gradual deceleration of the CR would combine to produce less change in heart rate than under the abrupt CS onset conditions used in the pretraining condition. Black and Black (1967) investigated the effect of various ISI in heart

rate conditioning with the rat. Although with some intervals their response measure was evidently confounded with responses to the UCS, in general, larger responses were obtained with longer CS - UCS intervals, up to at least five seconds. A decrease in response magnitude occurred above this duration. Examination of the data for the present experiment shows that the S with the largest responses to the thermal CS had a mean deceleration of 31.8 BPM for the first five trials of the fourth conditioning day. In comparison, this animal's response to the click CS on the final day of the experiment was a 65.6 BPM deceleration for the analogous five trial mean. Thermal CS presentations to this animal yielded no decelerations at 0.040 or 0.055 cal/sec/cm^2 radiation intensities, increases in skin temperature of 4.23 and 5.82°C respectively. The hypothesis of a high threshold to thermal radiation interacting with the gradual nature of the conditioned response accounts for the consistent but small decelerations in heart rate observed during the thermal CS training period. The large responses obtained from these same Ss when the click CS was presented after the termination of Condition H suggests that the daily exposure to the experimental situation was not in itself inhibitory.

Light CS: Condition L. Data from this condition indicate that the animals became conditioned with the gradual onset light CS. The result that this control group acquired

a CR supports the conclusion that the primary reason for the failure to find significant conditioning in the thermal CS condition is the insensitivity of the S's to the thermal CS rather than an inhibition caused by the transfer of training or the form of CS onset. The degree of heart rate change in Condition L was significantly larger than the maximum change occurring in Condition H, indicating a real difference in the effectiveness of these two stimuli in establishing CRs.

Conclusions. Electrophysiological researchers have not reported a significant number of afferent neurons in the rat which respond to small increases in skin temperatures. Previous behavioral investigations have resulted in ambiguous results or suggestions of low sensitivity. In this study, the animals did not establish conditioned responses to a thermal CS calculated to increase nose temperature 8.9°C, although only slightly larger temperature increases approach noxious levels of stimulation. This result is apparently unrelated to inhibitory effects of successive daily conditioning sessions, negative transfer from pretraining stimuli, or a general effect of a gradually increasing stimulus intensity. The failure of the animals to respond to the thermal CS seems to lie in the modality of this stimulus and its effectiveness as a stimulus to the species. It remains possible that warming sensitivity does exist in the Ss but large body areas must be stimulated to produce sufficient afferent activity for conditioning to occur. The data suggest

that if many receptors responsive to heat are to be found in the rat's nose, they are of low sensitivity, particularly in comparison to those of the cat, dog, or human. On the other hand, thermal pain response temperatures among these species is apparently similar.

APPENDIX

Figure 5

Sample data record, Experiment II. The three data segments form a continuous record. The upper trace indicates time marks and CS and UCS signal marks. The lower channel shows S's heart rate. The BPM difference between the twenty beat pre-CS and during CS intervals is a measure of the conditioned response. (Data from subject M, Condition L - 2, trial 19.)

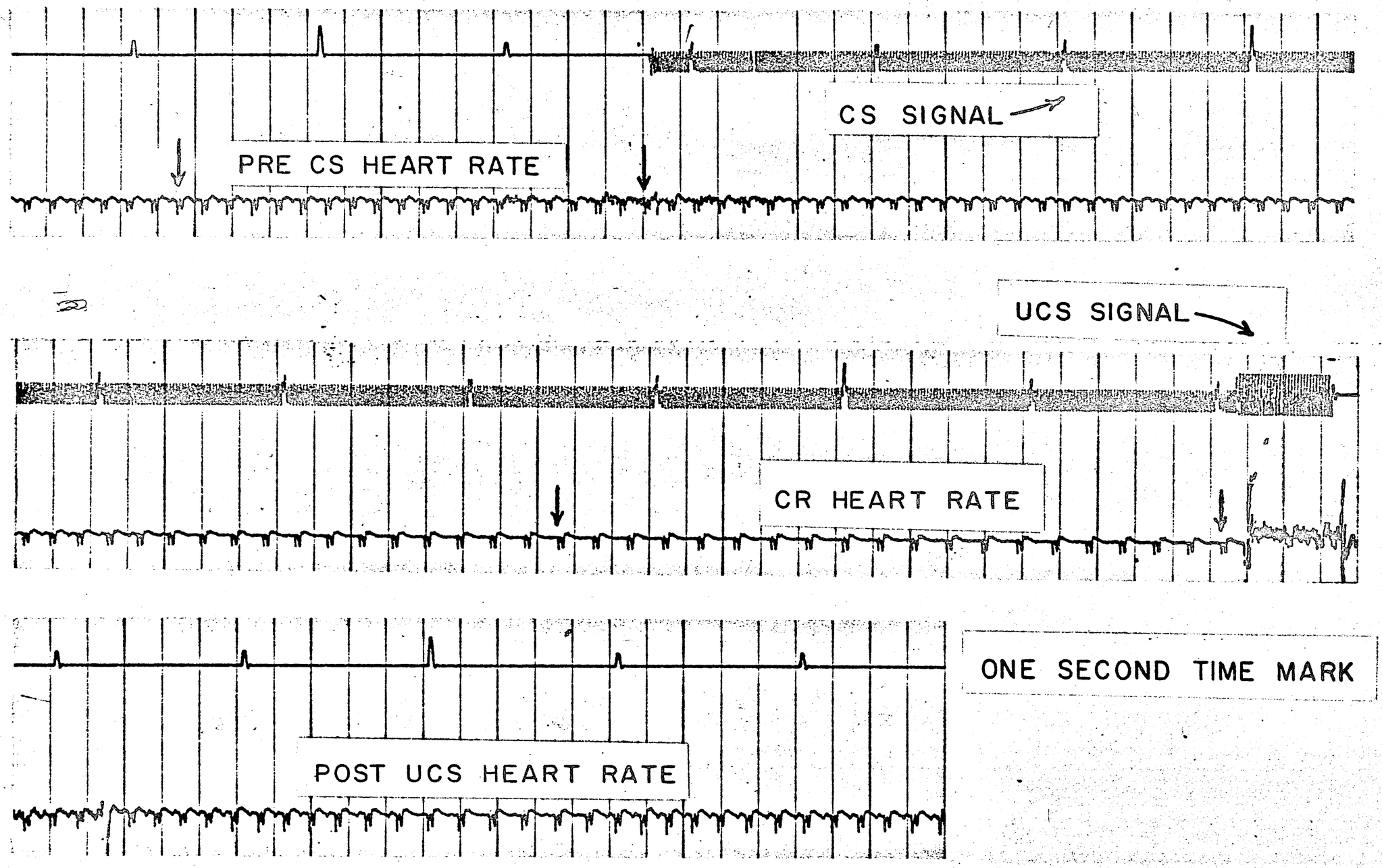

CS SIGNAL
PRE CS HEART RATE
UCS SIGNAL
CR HEART RATE
POST UCS HEART RATE
ONE SECOND TIME MARK

FIGURE 5

TABLE A

Experiment I: Escape Response Thresholds, Δ°C

Subject	Trial				
	1	2	3	4	5
	Q = 0.125 cal/sec/cm^2				
L	16.25	17.80	16.60	16.80	14.70
N	16.85	17.90	14.05	12.00	11.75
M	16.10	17.60	17.75	14.20	17.40
Q	10.90	14.45	18.75	15.40	13.35
K	15.25	14.70	14.50	12.25	12.90
$\bar{x}$	15.07	16.49	16.33	14.13	14.02
	Q = 0.1125 cal/sec/cm^2				
L	15.75	16.80	17.20	18.10	16.50
N	15.25	14.60	16.60	16.35	14.50
M	19.20	20.50	17.40	17.75	16.70
Q	16.55	15.15	14.10	17.10	14.00
K	18.15	20.40	18.10	13.40	15.10
$\bar{x}$	16.98	17.49	16.68	16.54	15.36
	Q = 0.100 cal/sec/cm^2				
L	17.85	15.80	18.55	16.60	16.90
N	18.05	14.05	11.60	16.15	17.50
M	17.30	14.70	17.80	17.60	14.40
Q	19.40	18.75	17.70	14.65	14.95
K	17.90	15.75	16.30	14.00	18.50
$\bar{x}$	18.10	15.81	16.39	15.80	16.45

TABLE B

Experiment II: Change in Heart Rate (BPM) for each S. (Five trial block means)

Parentheses indicate HR accelerations.

Subject	Block									
	1	2	3	4	5	1	2	3	4	5
	Condition C: CS Habituation					Condition C: Session 1				
S	4.82	27.45	(10.96)	18.19	(54.05)	(6.96)	(8.46)	3.02	7.45	(3.33)
T	(52.40)	4.17	(3.61)	3.00	(16.22)	15.48	(13.17)	3.49	8.18	25.92
P	(1.70)	(2.55)	(10.72)	1.68	7.62	0.00	4.58	10.59	9.76	8.14
J	12.38	(4.99)	(0.48)	(8.45)	(8.31)	16.92	15.98	7.78	8.00	(3.88)
F	4.16	(0.73)	(26.68)	1.88	(26.53)	34.21	46.81	35.58	9.41	0.00
$\bar{X}$	(6.55)	4.67	(10.49)	3.26	(19.50)	11.93	9.15	12.09	8.56	5.37
	Condition C: CS Habituation					Condition C: Session 1				
K	15.20	13.71	(31.56)	4.16	(2.46)	(8.98)	30.97	63.76	53.03	48.59
M	(1.57)	(0.88)	(17.91)	(18.82)	(3.99)	(13.79)	13.37	7.84	6.27	3.95
R	8.61	(8.88)	(1.48)	(7.11)	0.51	(6.75)	(2.36)	(2.21)	3.94	3.81
C	28.86	7.20	2.26	5.42	4.86	(8.17)	(9.85)	(23.54)	0.51	19.19
B	13.62	19.00	6.48	1.03	2.55	2.78	0.00	8.86	6.76	16.55
$\bar{x}$	12.82	6.03	(8.44)	(3.06)	0.29	(6.98)	6.43	10.94	14.10	18.42

TABLE B (continued)

Experiment II: Change in Heart Rate (BPM) for each S. (Five trial block means)

Parentheses indicate HR accelerations.

Subject	Block 1	2	3	4	5	1	2	3	4	5
	Condition C: Session 2					Condition H: CS Habituation				
S	63.27	54.18	34.40	35.24	0.00	16.66	15.40	(8.45)	(2.09)	(1.18)
T	49.07	37.13	8.93	50.46	11.98	19.84	1.59	2.80	1.89	(9.27)
P	33.51	22.49	17.34	6.73	4.76	(0.79)	(1.41)	0.32	(4.84)	3.02
J	27.34	22.69	55.70	38.40	19.80	(11.17)	(7.50)	10.25	(5.19)	(8.95)
F	76.46	66.04	60.09	36.68	50.15	6.94	(6.15)	10.98	4.11	3.18
$\bar{x}$	49.99	40.51	35.29	33.50	17.34	6.30	0.39	3.18	(1.22)	(2.64)
	Condition C: Session 2					Condition L: CS Habituation				
K	30.81	29.85	27.58	21.36	27.79	(28.82)	(4.28)	(1.87)	1.71	(3.25)
M	22.40	15.74	11.56	14.75	17.89	(5.57)	0.00	(1.86)	(24.65)	(2.17)
R	35.38	8.06	10.13	6.51	2.33	6.88	(16.41)	(6.25)	(14.12)	0.99
C	40.48	43.96	38.04	25.07	38.64	(17.31)	2.19	8.67	7.68	(3.36)
B	52.11	37.07	27.75	27.72	16.03	2.28	11.05	15.95	(1.56)	(3.59)
$\bar{x}$	36.24	26.94	23.01	19.08	20.54	(8.51)	(1.49)	2.93	(6.19)	(2.28)

TABLE B (continued)

Experiment II: Change in Heart Rate (BPM) for each S. (Five trial block means)

Parentheses indicate HR acceleration.

Subject	Block									
	1	2	3	4	5	1	2	3	4	5
	Condition H: Session 1					Condition H: Session 2				
S	13.10	2.99	11.01	22.10	4.20	(6.07)	8.08	(6.46)	6.84	(5.19)
T	1.06	(3.18)	7.11	(4.56)	(1.83)	17.93	7.39	14.66	1.51	(0.65)
P	19.54	(0.70)	(0.36)	1.91	1.90	6.19	4.23	(3.08)	9.39	13.45
J	2.02	1.62	12.51	1.69	1.14	12.54	4.87	6.63	(3.49)	4.67
F	0.62	13.79	11.13	6.58	0.00	(18.09)	0.00	17.96	1.81	0.00
$\bar{x}$	7.27	2.90	8.28	5.54	1.08	2.50	4.91	5.94	3.21	2.46
	Condition L: Session 1					Condition L: Session 2				
K	(0.39)	0.37	21.15	22.34	23.07	29.59	26.83	39.44	35.11	32.77
M	(4.09)	16.86	1.91	6.65	28.87	16.02	27.38	14.42	33.23	24.76
R	5.87	4.93	3.55	4.58	9.30	32.33	14.92	14.97	17.21	6.61
C	23.35	19.80	16.03	19.22	16.40	45.10	51.57	37.79	26.81	24.76
B	(0.74)	5.38	4.50	9.27	6.63	12.45	10.19	17.17	20.25	16.38
$\bar{x}$	4.80	9.47	9.43	12.41	16.85	27.10	26.18	24.76	26.52	21.06

TABLE B (continued)

Experiment II: Change in Heart Rate (BPM) for each S. (Five trial block means)

Parentheses indicate HR accelerations.

Subject	Block									
	1	2	3	4	5	1	2	3	4	5
	Condition H: Session 3					Condition H: Session 4				
S	0.00	1.70	3.20	11.53	0.00	6.24	1.27	7.97	9.80	6.77
T	12.02	25.87	1.68	(1.35)	(7.42)	0.00	(9.67)	4.63	(4.87)	0.65
P	20.37	12.58	9.38	5.16	10.52	31.03	22.38	6.84	16.66	5.38
J	0.00	22.98	(10.37)	4.44	0.45	31.79	14.95	7.38	20.92	6.96
F	2.91	(1.94)	5.11	(1.18)	(13.59)	11.67	13.24	2.99	(3.74)	18.75
$\bar{x}$	7.06	12.24	1.80	3.72	(2.01)	16.15	8.43	5.96	7.75	7.70
	Condition H: Session 5					Condition C: Recall Session				
S	(4.72)	(5.66)	(4.90)	0.00	4.80	32.45	17.64	23.81	29.02	23.84
T	(2.01)	6.43	(7.63)	(7.05)	2.10	18.12	26.37	(4.59)	(11.00)	38.50
P	24.95	12.95	8.30	14.28	10.31	76.43	28.56	27.90	29.06	31.47
J	23.08	17.74	(1.53)	10.89	12.63	65.61	49.69	22.67	21.69	7.21
F	6.39	5.09	2.31	7.62	0.43	17.53	33.84	30.66	29.09	34.03
$\bar{x}$	9.54	7.31	(0.69)	5.15	6.05	42.02	31.22	20.09	19.57	27.01

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