

memories may be accomplished by a complementary process. In this case the incipient positive memory activates the reward mechanism, which facilitates the act of retrieval.

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13. The idea that the act of memory retrieval has operant properties was developed in discussions with Dr. C. D. Wise.
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15. We thank J. Monahan, D. Massaro, and D. Leath for technical assistance.

9 May 1969; revised 14 July 1969

## Behavioral Regulation of Hypothalamic Temperature

**Abstract.** *Animals will work to produce changes in hypothalamic temperature. The two main inputs, skin and hypothalamic temperatures, combine to control this behavior. Specifically, the rate at which rats work for changes in hypothalamic temperature is proportional to the sum of the weighted displacements of skin and hypothalamic temperatures from their respective neutral values.*

Animals work for changes in skin temperature in response to displacements of either skin or hypothalamic temperature (1, 2). For example, rats work to turn on a draft of cool air when either skin or hypothalamic temperature is increased.

I now report that animals will also work for changes in hypothalamic temperature. The rate at which rats press a lever to produce reductions in hypothalamic temperature increases when either skin temperature ( $T_s$ ) or hypothalamic temperature ( $T_{hy}$ ) is increased above neutrality. When both inputs are varied,  $T_s$  and  $T_{hy}$  are additive, and  $T_s$  is given more weight than  $T_{hy}$  in the control of this behavior. Application of an additive linear model to the behavioral data permits direct quantitative comparison of the control systems for physiological and behavioral thermoregulatory responses.

Investigation of the interaction of  $T_s$  and  $T_{hy}$  in the control of behavioral adjustments of  $T_{hy}$  was made possible by the development of a general-purpose system (3) for studying thermoregulatory behavior in small mammals. The system incorporates a continuous flow of air over the body surface to control  $T_s$  and a water-perfused thermode implanted in the hypothalamus to control  $T_{hy}$ . Heat exchangers in conjunction with constant-temperature circulators provided stable control of air and water temperatures.

The animal is given control over either  $T_s$  or  $T_{hy}$  by arranging for its responses to activate a solenoid-operated valve in either the air or the hydraulic portion of the system. By pressing a lever, the animal produces an abrupt change in the temperature of either the air flowing over its body surface or of the water perfusing its hypo-

thalamic thermode, which causes an abrupt change in either  $T_s$  or  $T_{hy}$ . Thus the animal's choices between two values of  $T_s$  can be studied while  $T_{hy}$  is held constant, or its choices between two values of  $T_{hy}$  can be studied while  $T_s$  is held constant.

Thermodes (1, 3) consisting of a concentric arrangement of 18- and 22-gauge thin-wall stainless steel tubes were implanted in two adult, male Sprague-Dawley rats (T7 and T9). The thermodes were placed in the anterior medial preoptic areas. The following stereotaxic coordinates with the skull level between bregma and lambda were used, namely, 1.0 mm anterior to bregma; 0.5 mm lateral to the center of the superior sagittal sinus; and 8.5 mm down from the surface of the dura. Stainless steel machine screws in the frontal and parietal bones and dental acrylic cement were used to anchor the thermodes in place. A small (0.3 mm) thermistor bead attached to the outer surface of the thermodes 1 mm from the tip was used to measure  $T_{hy}$ .

About 1 week after the animals underwent surgery, the location of the thermodes was evaluated functionally. The animals were mildly restrained in still air at 25°C, and changes in  $T_s$  and rectal temperature caused by thermal stimulation of the hypothalamus were recorded. Both animals showed normal increases in  $T_s$  and decreases in rectal temperature when the hypothalamus was warmed. This indicates that the thermodes were located in or near the temperature-sensitive area and that the temperature sensitivity of the area had not been impaired by the placement of the thermode. In one animal, rat T7 (Figs. 1 and 2), the location of the thermode has been verified anatomically (4). In this animal, damage to the preoptic area was unilateral and was restricted to the anterior portion of one medial preoptic nucleus. The thermode was in contact with both medial preoptic nuclei, and the thermistor measured preoptic temperature.

Next, the animals were trained to work for reductions in ambient temperature. The temperature of the air flowing through the test chamber was normally warm (39°C), and the animal could reduce it to a neutral value (29°C) for 15 seconds by pressing the lever. After the animals mastered this task, as indicated by their stable rate of responding for reductions in ambient temperature, they were transferred to working for reductions in  $T_{hy}$ .

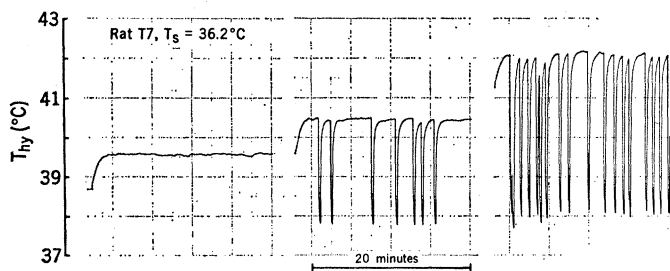
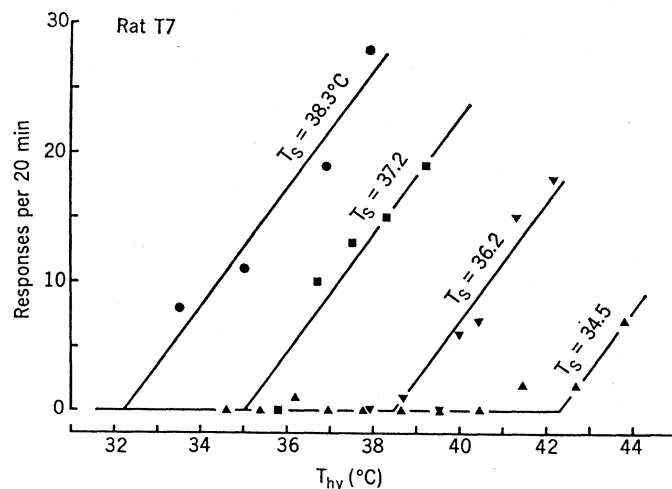


Fig. 1 (left). Strip-chart records of preoptic temperature from three 20-minute test periods during which skin temperature was held constant at 36.2°C. The rate of working for reductions in hypothalamic temperature ( $T_{hy}$ ) increases as hypothalamic temperature is increased. The wave form of the hypothalamic stimulus is shown. Fig. 2 (right). Interaction of skin and hypothalamic temperatures in the control of the rate of working for reductions in hypothalamic temperature. Each point is based on a 20-minute test; three such tests of the same animal are shown in Fig. 1. The data are summarized by  $R = 4.6[(T_{hy} - 39) + 2.8(T_s - 36)]$ .



During the tests in which behavioral adjustments of  $T_{hy}$  were studied,  $T_s$ , measured by a small (0.3 mm) thermistor bead on the dorsal surface of the base of the tail, was held constant by forced air convection. The animal's responses caused the thermal stimulator to switch from  $T_{hy1}$  to  $T_{hy2}$  for 15 seconds, thus producing transient reductions in  $T_{hy}$  after a delay of 2.5 seconds. The  $T_{hy}$  was initially set below the threshold value, and it was raised in approximately 0.5°C steps between successive 20-minute test periods. For values of  $T_{hy}$  above threshold, responses caused  $T_{hy}$  to fall to a value somewhat below threshold. Records of  $T_{hy}$  during three 20-minute tests of rat T7 (Fig. 1) show the wave form of the hypothalamic stimulus and indicate that when  $T_s$  is held constant, the rate of responding for reductions of  $T_{hy}$  is proportional to  $T_{hy}$ .

The interaction of  $T_s$  and  $T_{hy}$  was investigated in order to gain some understanding of the way in which signals arising from cutaneous and hypothalamic temperature receptors are integrated by the neural controlling system for thermoregulatory behavior. The rate of working for reductions in  $T_{hy}$  was determined during 20-minute tests at various combinations of  $T_s$  and  $T_{hy}$ . The ranges of values of  $T_s$  and  $T_{hy}$  explored in these experiments were 34° to 40°C and 32° to 44°C, respectively. The rate at which both rats worked for reductions in  $T_{hy}$  was increased by increasing either  $T_s$  or  $T_{hy}$  (Fig. 2). The similar slopes of the functions relating rate of responding to  $T_{hy}$  for each value of  $T_s$  indicate that signals arising from cutaneous and hypothal-

amic temperature receptors are integrated additively before the final common pathway for thermoregulatory behavior.

Additive linear models for the interaction of  $T_s$  and  $T_{hy}$  have been useful for interpreting the control of behavioral adjustments of  $T_s$  (1) and a variety of physiological thermoregulatory responses (5). The thermoregulatory response ( $R$ ) is assumed to be proportional to an error signal which is the sum of the weighted displacements of  $T_s$  and  $T_{hy}$  from their respective neutral values,  $T_{s0}$  and  $T_{hy0}$ . Thus,

$$R = a[(T_{hy} - T_{hy0}) + b(T_s - T_{s0})]$$

where  $a$  is the slope constant and  $b$  is the weighting constant expressing the relative importance of  $T_s$  in the determination of the magnitude of the response. This model provides an excellent summary of the control of behavioral adjustments of  $T_{hy}$  in rats T7 and T9 (6).

The fact that an additive linear model applies to the control of both physiological and behavioral thermoregulatory responses suggests a basic similarity between the controlling systems for the two kinds of response. There is, however, an important difference between the two controlling systems.

Parameter estimation procedures (7) yielded estimates for the values of the constant  $b$  of 2.8 and 2.2 for rats T7 and T9, meaning that  $T_s$  is given between two and three times as much weight as  $T_{hy}$  in the control of the rate of working for reductions in  $T_{hy}$ . The relatively greater role of  $T_s$  ( $b > 1$ ) in the control of behavioral adjustments of

$T_{hy}$  is to be contrasted with the relatively greater role of  $T_{hy}$  ( $b < 1$ ) in the control of physiological thermoregulatory adjustments (8).

The greater emphasis apparently given to  $T_s$  in the control of behavioral thermoregulatory responses is appropriate to the anticipatory function of thermoregulatory behavior. That is, the function of behavioral thermoregulatory responses is to escape from or to avoid external thermal stress immediately upon its detection by cutaneous thermal receptors and before it disturbs internal body temperature. By escaping from and avoiding temperature extremes, the animal selects a thermally neutral environment where fine control of internal body temperature can be accomplished by minimum activity on the part of the automatic physiological thermoregulatory responses.

The experiments described here indicate (i) that when  $T_s$  and  $T_{hy}$  are the only variables the drive for thermoregulatory behavior may be identified with the thermal error signal  $(T_{hy} - T_{hy0}) + b(T_s - T_{s0})$ , and (ii) that a drive induced by changes in either  $T_s$  or  $T_{hy}$  can be reduced by changes in  $T_{hy}$  as well as by changes in  $T_s$  as shown previously. These experiments support earlier work in showing that both  $T_s$  and  $T_{hy}$  contribute to thermal discomfort (9), and they suggest furthermore that thermal discomfort resulting from displacement of either  $T_s$  or  $T_{hy}$  can be alleviated by changes in  $T_{hy}$  as well as by changes in  $T_s$ .

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7. An estimate of  $T_{s_0}$  was obtained empirically by increasing ambient temperature from 30°C at a rate of 0.3°C per minute, and determining the value of  $T_s$  at the moment when the animal first pressed the lever to reduce ambient temperature to 29°C;  $T_{s_0} = 36^\circ\text{C}$ . The  $T_{hy}$  was free to vary and approximately 39°C during these tests. The estimate of  $T_{s_0}$  is needed to estimate  $T_{hy_0}$ , the x-intercept when  $T_s = T_{s_0} = 36^\circ\text{C}$ ;  $T_{hy_0} = 39^\circ\text{C}$ . The constant  $a$  is simply the average slope constant obtained by the method of least squares;  $a = 4.6$  and  $1.1$  responses per 20 minutes for 1°C for rats T7 and T9. Given estimates for  $T_{s_0}$ ,  $T_{hy_0}$ , and  $a$ , it is possible to solve for  $b$ .
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10. Supported by NIH research grant MH-16608.

4 June 1969; revised 17 July 1969

## Controversial Taxonomy of Fossil Hominids

Leakey, Protsch, and Berger (1) included, in a table, four questionably valid names for fossil hominids. Later Brace (2) questioned the continued unqualified use of two of these names, "*Homo leakeyi*" and "*Homo habilis*," and Leakey *et al.* then replied (3). A few further comments seem warranted because Leakey *et al.* have not really answered Brace's criticisms.

Concern over the citation and justification of "*Homo leakeyi*," a name founded on Olduvai hominid 9, is warranted because any further use of this name is an error in view of its originally having been proposed conditionally. In 1963 Heberer (4) remarked: "Als Vorschlag, der nicht vorgreifen will, möge die folgende Benennung gewertet werden: 1. *Homo leakeyi* n. sp. oder 2. *Homo erectus leakeyi* n. subsp."

According to the *International Code of Zoological Nomenclature* (article 15) names proposed conditionally after 1960 have no taxonomic validity and are to be considered *nomina vana* (5). Irrespective of the name's being invalid on this technical point, however, the *calvaria* itself appears to differ from Java man (*H. erectus*) no more than does Pekin man (*H. erectus*). In 1966, after "*H. leakeyi*" was conditionally

proposed, Leakey himself (6) referred to this *calvaria* as *H. erectus*. Evidently Leakey has now changed his position again because Leakey *et al.* in their reply to Brace have omitted the name "*Homo leakeyi*" from their Table 1 which they say indicates their "own choice" of names for the fossils in question. Unfortunately, however, if these authors no longer intend to use "*Homo leakeyi*," the (apparent) substitution of the term "*Pithecanthropus* sp." can hardly be considered an improvement. This latter genus is now almost universally accepted as a junior synonym of *Homo*.

The validity of "*Homo habilis*" poses a more complicated problem which can only be touched on here. The two papers cited by Leakey, Protsch, and Berger, in our opinion, do not go a long way toward answering any challenge to the validity of "*Homo habilis*," if for no other reason than their having failed to treat adequately the objections raised by Robinson (7). In fact one of these papers supposedly validating the name (6) makes no reference to the type specimen of "*Homo habilis*." Three points about the "*Homo habilis*" material remain to be convincingly demonstrated. These are (i) that the type

mandible (Olduvai H. 7) and other material from bed I (Olduvai H. 8) samples a population which is specifically distinct from South African *Australopithecus africanus* populations, (ii) that the bed II material should be referred to the same species as the bed I material, and (iii) that the bed I and bed II material whether taken separately or together should be placed in genus *Homo* and not in *Australopithecus*.

Some of the "unwarranted name-giving" referred to by Brace might have been avoided had the placement of the "*Homo habilis*" material originally been assessed rigorously. To this end we suggest that the following procedures be applied when the taxonomic position of new hominid fossil finds is under consideration:

1) The material should first be compared with the most closely similar, previously described species which are roughly contemporaneous with it.

2) If it is considered distinct at the specific level from these materials, the next step is to determine in which lineage the new species belongs.

3) The placement of a new species in a lineage having been determined, the problem remaining is to decide at which points within the lineage specific and generic distinctions are warranted. This is partly a subjective matter, but the range of variation within a taxon should be determined, where possible, by analogy to the range of variation within species and genera of present-day related forms. Where this scheme cannot be applied because of inadequate information, new specimens should remain unnamed, or be tentatively referred to prior taxa pending accumulation of more data relevant to their status.

The bed I "*Homo habilis*" material, in fact, closely resembles *Australopithecus* sp. from South Africa. The mandible and teeth are very similar to those of *A. africanus*. The parietals indicate a brain volume well within the calculated *Australopithecus* population range, but falling near the lower extreme of the calculated range for *Homo*. The hominid 8 talus (associated at the same site as the type of "*Homo habilis*") appears to have functional affinities with the Kromdraai talus, and these two are much more similar to one another than either is to *Homo sapiens* on the one hand, or to any pongid on the other (8). Likewise, the hominid 8 clavicle is said (9) to differ somewhat from the clav-