permeabilities of submitochondrial particles to perchlorate and thiocyanate (*1*). The histogram illustrates the large disparity between the permeability of the biological membrane and that of PC-decane bilayers to these ions. Differences in bilayer thickness may account for some of the discrepancy, as shown by the permeability of solvent-free PC bilayers. The increased dielectric constant of the PC-chlorodecane bilayers, however, has a much greater effect on permeability, especially when perchlorate is the permeant ion.

To reconcile the ability of weak acids to transport protons across artificial phospholipid bilayers with their ability to uncouple oxidation from phosphorylation in mitochondria, we previously postulated (*6*) that some fraction of the lipid bilayer component of the inner mitochondrial membrane has a dielectric constant greater than 2.2. The data presented in Fig. 2 are consistent with this postulate.

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3. Some experiments were performed with a mixture of lipids chosen to mimic the lipid composition of the inner mitochondrial membrane; 40 percent phosphatidylethanolamine, 40 percent phosphatidylcholine, and 20 percent cardiolipin (by weight). The thiocyanate permeabilities of solvent-free, decane-containing, and chlorodecane-containing bilayers made with these lipids are within a factor of 2 of the conductances of the analogous bilayer made with PC (see Fig. 1).
4. The first term in Eq. 1 is the Born expression for two semi-infinite media; the second term is a correction for the finite thickness of a lipid bilayer [A. Parsegian, *Nature (London)* **221**, 844 (1969)].
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8. The PC was dried from a chloroform solution with nitrogen, mixed with an appropriate volume of decane or chlorodecane, then combined with a saline solution containing 0.1*M* NaCl adjusted to *p*H 7.4. The lipid-alkane-saline suspensions were thoroughly mixed, equilibrated for several hours, sealed in quartz-glass x-ray capillary tubes, and mounted in a flat-plate x-ray camera. Measurements and analysis were performed as described by T. J. McIntosh [*Biochim. Biophys. Acta* **513**, 43 (1978)].
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10. Deviations from linearity are noted at concentrations higher than those reported here. These deviations are due to electrostatic effects (*2*).
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12. Diphytanoylphosphatidylcholine swells in saline in a manner similar to the swelling of egg lecithin [D. M. Small, *J. Lipid Res.* **8**, 551 (1967)]. The lamellar x-ray repeat period increased with increasing concentration of either decane or chlorodecane, up to a hydrocarbon mole fraction of 0.8. The repeat period did not increase further, indicating that excess alkane is present when the mole fraction of hydrocarbon is greater than 0.8. The average lamellar repeat period for PC in excess saline is 64 ± 1 Å, whereas the repeat period with PC with excess saline and excess (0.9 mole fraction) alkane is 104 ± 6 Å for decane and 97 ± 3 Å for chlorodecane (three and four experiments, respectively). Additional evidence that decane and chlorodecane affect the bilayer structure in a similar manner was obtained by differential scanning calorimetry. At equal concentrations, the two organic solvents had similar effects on the dipalmitoyl lecithin phase transition: they lowered and broadened the transition.
13. The permeabilities of solvent-free PC and PC-decane bilayers to perchlorate, on the other hand, differ by less than a factor of 10 (Fig. 2). Others have also noted that the dependence of permeability on thickness predicted by Eq. 1 is not observed with all ions [A. D. Pickar and R. Benz, *J. Membr. Biol.* **44**, 353 (1978)]. Factors not included in Eq. 1, such as the polarizability of the ions and the inhomogeneity of the dielectric constant, must also be important.
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15. It should be noted, however, that smaller effects are observed when the halogen groups are fixed to the lipid chains rather than to the alkane solvent. A solvent-free membrane was formed from a 1:1 mixture of PC and 1,2-di-(10-bromosteroyl)phosphatidylcholine [M. A. Roseman, B. R. Lentz, B. Sears, D. Gibbes, T. E. Thompson, *Chem. Phys. Lipids* **21**, 205 (1978)]. Compared to solvent-free PC membranes, the capacitance was enhanced by 10 percent and the permeabilities to perchlorate and thiocyanate were enhanced by a factor of about 3.
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Microwaves: Effect on Thermoregulatory Behavior in Rats

Abstract. *Rats, with their fur clipped, pressed a lever to turn on an infrared lamp while in a cold chamber. When they were exposed to continuous-wave microwaves at 2450 megahertz for 15-minute periods, the rate at which they turned on the infrared lamp decreased as a function of the microwave power density, which ranged between 5 and 20 milliwatts per square centimeter. This result indicates that behaviorally significant levels of heating may occur at an exposure duration and intensities that do not produce measurable changes in many other behavioral measures or in colonic temperature. Further study of how microwaves affect thermoregulatory behavior may help us understand such phenomena as the reported "nonthermal" behavioral effects of microwaves.*

Reports of "nonthermal" behavioral effects of microwaves have contributed to debates about the safety of microwaves. There is no question that microwaves can affect behavior (*1*). Microwaves heat tissue, and heat itself can affect behavior (*2*). When microwaves increase colonic temperature, concomitant behavioral changes are often attributed to the thermal burden (*3*). When microwaves produce no observable changes in colonic temperature, concomitant behavioral changes are sometimes attributed to "nonthermal" actions of microwaves, especially by Soviet and Eastern European investigators (*4*). Numerous biological processes, however, are affected by local temperatures that are not highly correlated with the core temperature (*5*); indeed, many help ensure its constancy. Thermoregulatory behaviors, those behaviors that directly affect, and are often controlled by, the thermal environment of the subject, generally respond to skin and hypothalamic, rather than colonic, temperatures (*6*-*8*). It seems plausible, then, that microwaves might alter behavior as a consequence of thermal stimulation in the absence of measurable core temperature changes.

Current techniques for measuring temperature changes in animals exposed to microwaves are inadequate for several reasons: (i) sensitivity is limited to about 0.1°C; (ii) ongoing thermoregulation serves to dissipate heat; (iii) "hotspots," that is, localized increases in temperature, can occur at locations not being monitored; (iv) most sensors distort the microwave field. Finally, since any absorption produces some temperature increase, it is still necessary to determine its functional significance. One way to avoid these difficulties is to use the organism's behavior as the thermometer, so to speak.

Six male Long-Evans hooded rats (325 to 450 g) were individually trained to press a small lever in order to turn on an infrared lamp for 2 seconds. Responses made during the 2-second period produced no programmed consequences. Test sessions, each of approximately 24 hours, started late in the afternoon. At this time, the fur of the rat was clipped, and the rat was placed in a chamber (*9*) located in a dark, refrigerated room (see Fig. 1). After a few such sessions, the rat generally pressed the lever at a nearly constant rate for several hours. This performance provided a baseline for studying the effect of 2450 MHz continuous-wave (CW) microwaves on thermoregulatory behavior. For sessions in which microwave exposure (*10, 11*) was scheduled, the first control period began in the morning after the rat had been in the chamber for several hours. Alternating control and exposure periods lasted 15 minutes each. Within a single session, across different exposure periods, the microwaves illuminated the chamber either in an ascending followed by a descending series or in a descending followed by an ascending series of power densities.

Figures 2 and 3 show the results of exposing rats to 2450-MHz CW microwaves (*12*). Figure 2a shows that the proportion of time during which the heat lamp was kept on decreased as the microwave power density increased. Figure 2b confirms this relationship by showing a decrease in the ratio of the lamp-on time during an exposure period to the lamp-on time during the preceding control period. Figure 3 shows cumulative records of lever presses that turned on the heat lamp. The slopes of the records remained fairly constant within individual exposure and control periods, demonstrating that the consequences of presentation or removal of microwaves were immediate and constant throughout the respective condition. These data indicate that rats turn on the heat lamp less frequently during a 15-minute period of exposure to microwaves than during control periods; that the decrease is a direct function of power density; that it appears almost immediately; that it occurs at 5 mW/cm^2; and that recovery follows immediately after each exposure.

Statistical analyses support these conclusions. A linear regression model provided a close fit to the data (*13*). Individual regression lines for the five rats with complete data had nonzero slopes ($P < .01$, *t*-test). By calculating the coefficient of determination (r^2; the percentage variation determined by power density) we obtained the following values for each rat: MW14, 63; MW17, 81; MW21, 70; MW22, 76; and MW24, 83 percent. The usual assumptions of homogeneity of variance and normal distribution of errors were checked. An analysis of covariance demonstrated that the individual regression lines of heat lamp on time to power density had different intercepts, $F(4,50) = 11.54$, $P < .01$, but not different slopes, $F(4,54) = 0.79$. By analysis of r^2 we found that this model accounted for 79 percent of the variance. The common slope (− 0.0062) indicates that if one views microwaves as replacing heat from the lamp, then the amount of heat replaced by a given power density is the same for each rat (*14*).

The most reasonable interpretation of these data is that the rat responds to maintain a nearly constant thermal state (*15*). When heat from one source, microwaves, is introduced, the rat compensates by reducing the heat contributed by another source, the infrared heat lamp. The sensitivity of the rat to relatively small changes in power densities under this procedure, compared to most others used to study behavioral effects of microwaves (*16*), as well as the immediate recovery during the control periods, support this view. Thermoregulatory behavior, therefore, may provide an index of the thermal burden contributed by microwaves. Even if measurable colonic temperature change may sometimes occur at 5 mW/cm^2, the observed time course of the behavior change does not parallel it (*11, 17*). Thermoregulatory behavior responded immediately to thermal change (*18*).

In this experiment we measured one thermoregulatory behavior directly, but obviously such behaviors occur whether or not one measures them. Furthermore, they occur concurrently with other behaviors (*19*). Changes in the frequency of thermoregulatory behaviors, such as reduced activity, sprawling, and saliva spreading, could provoke changes in the frequencies of these other behaviors. Interpretations of reported "nonthermal"

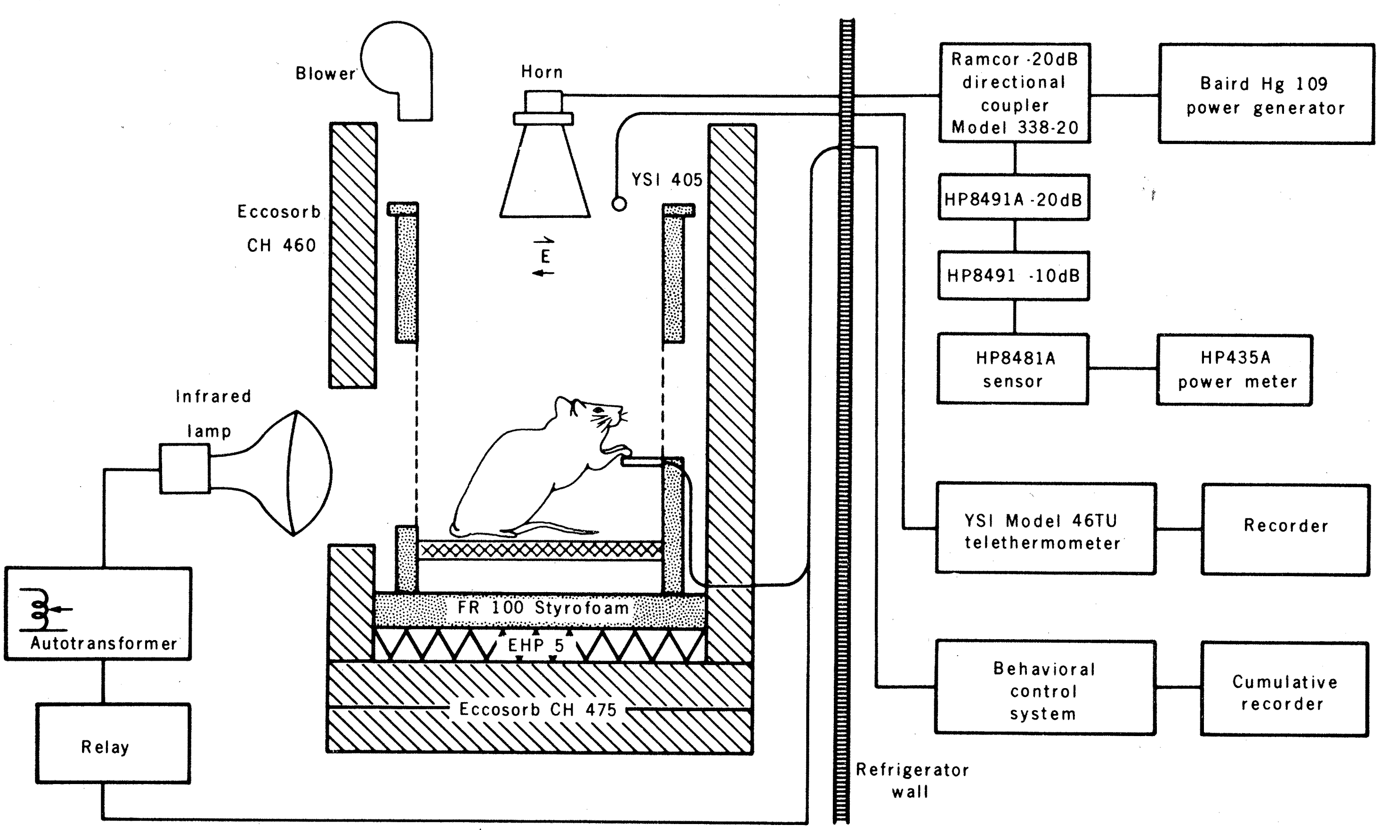

Fig. 1. The system for studying the effect of microwave exposure on thermoregulatory behavior. The rat, with its fur clipped, could turn on the infrared lamp for 2 seconds by pressing the lever. Microwaves were presented on a schedule independent of the rat's behavior.

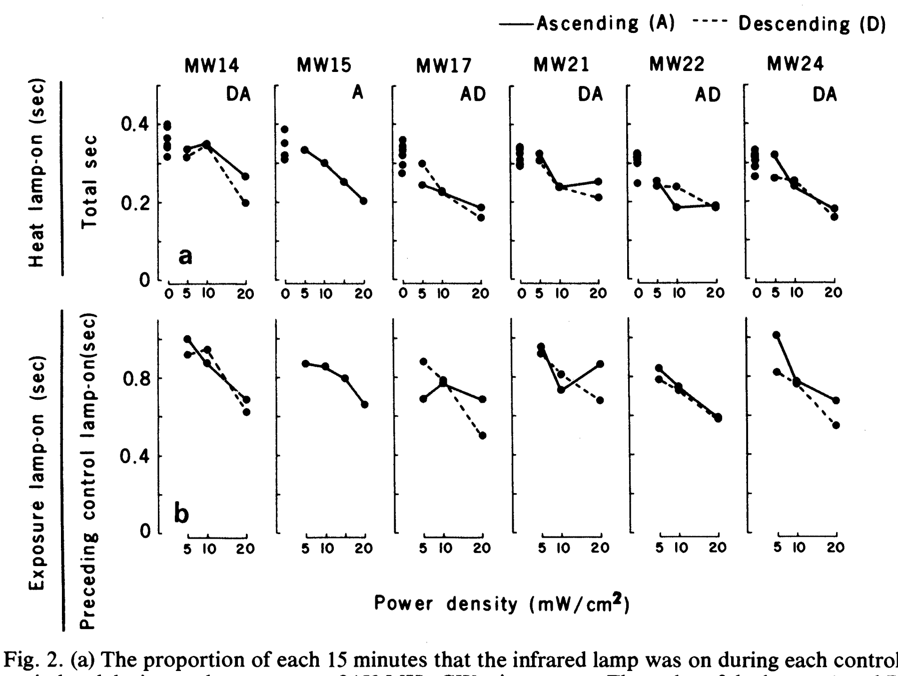

Fig. 2. (a) The proportion of each 15 minutes that the infrared lamp was on during each control period and during each exposure to 2450 MHz CW microwaves. The order of the letters *A* and *D* designates the sequence of the ascending (*A*) and descending (*D*) series of power densities. (b) The ratio of the proportion of each 15-minute microwave-exposure period that the infrared lamp was on to the proportion of the immediately preceding 15-minute control period that the infrared lamp was on. A ratio of less than 1.0 indicates that the rat turned the infrared lamp on less frequently during exposure to microwaves than during the preceding control period (MW14, MW15, and so on, refer to individual rats).

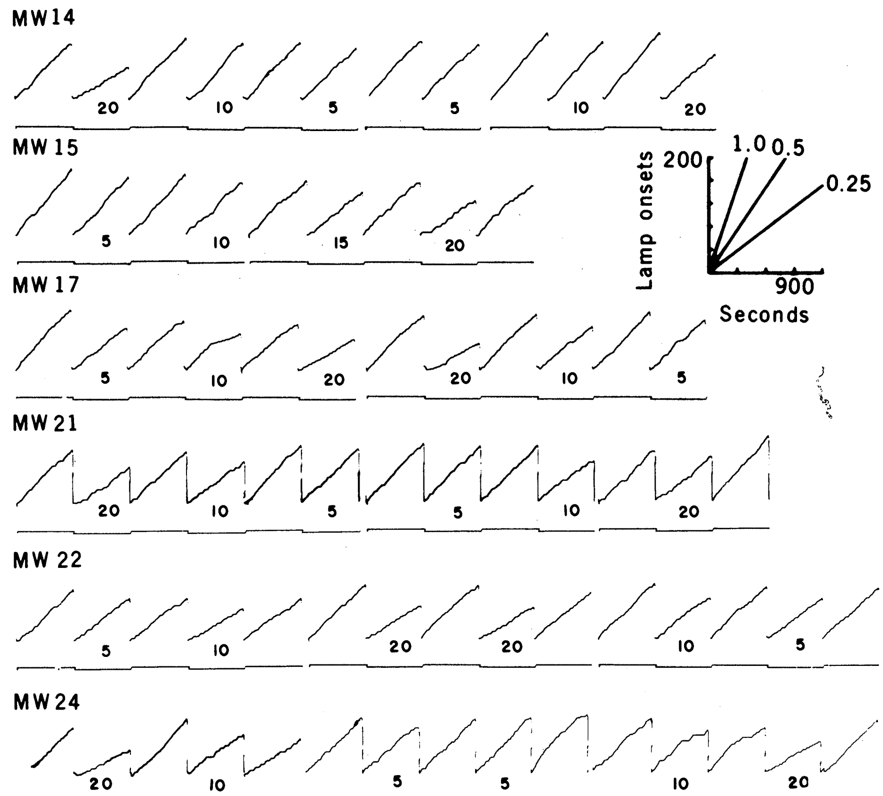

Fig. 3. Cumulative records showing the rate at which rats turned on the infrared lamp during the same exposure periods and in the immediately preceding control periods, from which the data of Fig. 2, a and b, were obtained. Records from additional periods after exposure also show the recovery of responding. The chart speed was constant. Each lever press that turned on the infrared lamp moved the upper pen vertically. Since the lamp could be turned on at a maximum rate of once every 2 seconds, the slope of the record shows the proportion of time the lamp was on. The inset shows the proportion of selected slopes. The upper pen was reset at the end of each 15-minute period. The lower pen was deflected downward during the exposure period. The power density of each exposure is indicated above the lower channel. Note that rat MW15 was exposed only to an ascending series of power densities.

behavioral effects of microwaves might be clarified if concurrent thermoregulatory behaviors were recorded.

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6. Thermoregulatory behavior is sensitive to numerous variables including the following: ambient temperature; internal temperature; magnitude or duration of reinforcement, or both; species; age; metabolic state; drugs; chemical or electrolytic brain lesions; and behavioral requirement for temperature change. For reviews, see Weiss and Laties (*7*); Carlisle (*8*); J. D. Corbit, in *Physiological and Behavioral Temperature Regulation*, J. D. Hardy, A. P. Gagge, J. A. J. Stolwijk, Eds. (Thomas, Springfield, Ill., 1970), p. 777; D. Murgatroyd and J. D. Hardy, in *ibid.* p. 874; Satinoff and Henderson (*2*).
7. B. Weiss and V. G. Laties, *Science* **133**, 1338 (1961).
8. H. J. Carlisle, in *Animal Psychophysics: The Design and Conduct of Sensory Experiments*, W. C. Stebbins, Ed. (Prentice-Hall, Englewood Cliffs, N.J., 1970), p. 211.
9. The chamber (20.4 by 20.8 by 40.5 cm) was constructed out of FR 100 Styrofoam foamed polystyrene that is transparent to 2450 MHz microwaves [V. R. Reno and J. O. de Lorge, *IEEE Trans. Biomed. Eng.* **24**, 201 (March 1977)]. Windows (15 by 25 cm) on three sides, each lined with 0.0127-cm cellulose acetate, allowed transmission of radiant energy. The fourth side, which contained the response lever, was lined with Mylar to reduce damage by gnawing and scratching. Nylon mesh in a Styrofoam frame served as the cover. An acrylic lever (2.6 cm wide and 0.32 cm thick) protuded 5 cm into the chamber 4 cm above the polystyrene grid floor. The lever, mounted on a metal base attached to the outside wall, contained a microswitch for detecting lever presses. The inside of that wall was located 44 cm from the front of the 250 W infrared lamp that was operated at 130 V a-c. The temperature decreased intermittently to approximately 1.1°C. It recovered quickly to approximately 3.6°C and over the next 2 to 3 hours in-

creased at an approximately linear rate to 5.5°C. Control and exposure data were obtained between 3.9° and 5.3°C. A blower (100 ft^3/min) provided airflow from above. The airflow, measured below the empty chamber with a hot-wire anemometer (Datametrics Airflow Multimeter Model 800 VTP), was approximately 6 m per minute in the region of the lever and increased to approximately 18 m per minute at the opposite side of the chamber.

10. Microwaves were transmitted to the horn via a coaxial cable to a coaxial-waveguide adapter. The feeder horn with a 6.5 by 7.5 cm rectangular aperture directed the microwaves toward the chamber floor 44.5 cm below with the E field parallel to the axis established by the response lever and infrared lamp. The designated power density specifies that value at the lever. A Narda Model 8315 probe calibrated against an NBS XD-1 probe was used to map the field. With the back wall removed, the field was measured at the level of the lever at nine locations in a 10 by 10 cm grid with loci 5 cm apart covering the central area of the chamber. The distribution of power densities varied within 11 percent of the mean value. The field was also mapped with a smaller probe fabricated by J. Ali (U.S. Environmental Protection Agency) which enabled measurements to be made at loci close to the chamber walls. There was close correspondence between the two sets of measurements. The energy absorption rate per unit mass was estimated according to the relationship $P = 4.186\, C\Delta T/t$, where C is the tissue specific heat in calories per gram per degree Celsius (in this analysis, $C = 0.83$), ΔT is the temperature increase in degrees Celsius, t is the duration of exposure in seconds, and P is watts per kilogram [C. C. Johnson, *J. Microwave Power* **10**, 249 (1975)]. A YSI 423 probe inserted 6 cm into the colon measured the temperature of a pentobarbital-anesthetized rat encased in a Styrofoam block during a brief exposure to microwaves [Lu *et al.* (*11*)]. Delta-t, the rate of temperature change, included a correction for the rate of temperature change immediately preceding the exposure. The absorption rate was approximately 8.4 W/kg at a power density of 41 mW/cm^2, resulting in a specific absorption rate of 0.20 W/kg per milliwatt per square centimeter.
11. S.-T. Lu, N. Lebda, S. Michaelson, S. Pettit, D. Rivera, *Radio Sci.* **12(S)**, 147 (1977).
12. These data are the results of the second exposure session. After studying three rats, we found that the results from the first session were similar to but more variable than those from the second. Since such an outcome might be attributable to the novelty of the microwaves, an effect often seen during initial exposure to drugs and other stimuli, we decided to focus on the data from the second sessions of those three rats plus three others. The following are the means (standard errors in parentheses) of the proportion of time the heat lamp remained on at each power density for all six rats. For the first exposure session: 0 mW/cm^2, 0.364 (0.017); 5 mW/cm^2, 0.333 (0.040); 10 mW/cm^2, 0.324 (0.032); and 20 mW/cm^2, 0.273 (0.029). For the second exposure session: 0 mW/cm^2, 0.326 (0.009); 5 mW/cm^2, 0.298 (0.015); 10 mW/cm^2, 0.264 (0.020); and 20 mW/cm^2, 0.199 (0.011). Thus the two functions are similar, but the variability from the second session is less, as would be expected, after previous experience.
13. Serial correlation within individual rats was examined by the Durbin-Watson test [J. Neter and M. Wasserman, *Applied Linear Statistical Models* (Irwin, Homewood, Ill., 1974)], which confirmed the absence of an effect from the previous 15-minute exposure and the suitability of the linear regression model.
14. Using randomization tests [A. R. Feinstein, *Clinical Biostatistics* (Mosby, St. Louis, 1977)] we compared results for the six rats at each power density with all control periods, with only the preceding control period, and with the adjacent exposure to a different and nonzero power density. Two-sided P values were less than $P = .003$ except for 5 mW/cm^2 against all zero exposures and 5 mW/cm^2 against adjacent 10 mW/cm^2 ($P = .02$). These results provide additional confirmation of the sensitivity of the procedure as well as an independent check of the regression analysis.
15. That interpretation is consistent with the conclusion reached in numerous studies of behavioral thermoregulation, including those of Weiss and Laties (*7*) and Carlisle (*8*).
16. See N. W. King, D. R. Justesen, and R. L. Clarke [*Science* **172**, 398 (1971)] for an example of a different sensitive procedure. We did not attempt to determine the limits of the sensitivity in the present study; instead, we wanted to determine if the thermal action of microwaves could produce behavioral change in the absence of reliable, measurable changes in colonic temperature.
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18. Although a compensatory change in behavior occurs, we do not know if the overall absorbed heating is constant across conditions. Certainly, the spatial distributions of absorbed energies differ between microwaves and infrared heat. The relationship between electromagnetic energy and transduced thermal energy is complex. For example, see R. A. Tell, *An Analysis of Radiofrequency and Microwave Absorption Data with Consideration of Thermal Safety Standards* (U.S. Environmental Protection Agency Tech. Note No. ORP/EAD 78-2, Washington, D.C., April 1978). For present purposes it is sufficient to assume at least an ordinal relationship between the two.
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20. We thank C. Cox and H. T. Davis for the statistical analyses, and C. A. Wallen for criticism of the manuscript. We thank J. Ali and EPA for assistance in mapping the microwave field. This paper is based on work supported in part by postdoctoral fellowship F22 ES01804 (awarded to S.S.) and grant ES-01247, both from the National Institute of Environmental Health Sciences, and in part by a contract with DOE at the Department of Radiation Biology and Biophysics, University of Rochester, and is Report No. UR-3490-1537.

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Chimpanzee Problem Comprehension: Insufficient Evidence

Premack and Woodruff (*1*) showed a chimpanzee (Sarah) videotaped scenes of a human actor struggling with problems. The video image was then frozen and Sarah picked one of two photographs as a "solution" to the actor's problem. Sarah's performance on this task was said to have permitted examination of "the animal's knowledge about problem-solving—its ability to infer the nature of problems and to recognize potential solutions to them" (*1*, p. 532).

Premack and Woodruff do not present any evidence, independent of Sarah's choice of photographs, to indicate (i) that she saw the videotaped sequences as problems to be solved, (ii) that she perceived her choice as representing a solution to the portrayed problem, and (iii) that she understood either the elements of the problems or the nature of the solutions or if faced with the problem that she could solve it herself. These factors cannot be presumed to be the inherent bases for Sarah's choices of photographs unless it is independently demonstrated that the scenarios were, in fact, problems in Sarah's perception and that she understood their video presentation. Failure to demonstrate this allows for the possibility that the dynamics of the scenarios were beyond Sarah's comprehension and that her choices of alternative photographs were based on simpler strategies than those suggested by Premack and Woodruff. If the scenarios were not perceived as problems by Sarah, then her choices obviously could not have been solutions.

On what other basis might Sarah have selected the alternatives which she did? It seems reasonable to conclude, given the variety of previous training paradigms which Sarah has received, that she could have used relatively simple match-to-sample strategies, none of which would require an understanding of either the problems portrayed in the videotape or that her choices represented solutions. For instance, it is clear, from the video stills and photographs presented by Premack and Woodruff (*1*, p. 533), that problems 1 and 2 of the banana-attainment series could readily have been solved by a straightforward matching response of the photograph to the scene held on the monitor on the basis of physical similarity of the images themselves. Problems 3 and 4 present a more difficult match-to-sample choice; however, Sarah performed at chance on these.

Problems 5 to 8 were object-choice tasks in which Sarah was to pick a photograph of an object which could be used to solve the actor's problem. This group of problems could have been solved by selecting the item (key, faucet, and so forth) that had been most frequently associated with the sample object (lock, hose) on the basis of past observational experience (*2*).

The single subject of this study, Sarah, had received extensive training involving both physical match-to-sample and associative match-to-sample tasks. The format of the frozen-video paradigm selected by Premack and Woodruff is virtually identical to the subject's past match-to-sample training and could thereby be expected to produce a "set" toward this type of response.

Testwise chimpanzees can readily learn a series of paired-choice problems on the basis of the first trial's correct-