plays a role in attention, and two symptoms have been described that bear on our results. The first symptom is a restriction in attention to only the most salient features of a stimulus (6); the second symptom is a difficulty in learning a less salient dimension when a more salient dimension is present and irrelevant (7). When viewed in terms of the salience of the stimulus dimensions, both symptoms seem to reflect a single deficit; but, when looked at in terms of our distinction between perseveration and distractibility, a different conclusion is suggested. The first symptom fits our picture of a tree shrew deprived of temporal cortex inasmuch as we would expect such a preparation to produce failure to notice less salient dimensions. But the second symptom could well apply to our animals with striate lesions, since their difficulty might be described as a failure to attend to a less salient dimension (pattern) when distracted by a more salient dimension (hue). Since we now know that the inferotemporal area of the monkey contains two functional subdivisions, we cannot help wondering whether the lesions in the two experiments cited differed in their rostral-caudal extent; the first symptom might be related to the rostral sector and the second symptom to the caudal sector (8). But if the visual cortex has undergone further differentiation between the evolutionary stages represented by tree shrew and monkey with the result that *three* main centers have replaced two, is there any good reason to assume that the subdivision of psychological functions present in the earlier stages will be preserved in the later stages? For example, we may ask whether the functional distinction between striate and temporal areas found in the tree shrew corresponds to separate centers throughout vertebrate history. The answer is almost certainly No, since there must have been a time in vertebrate history when the visual system had only one mechanism of control and integration, probably the optic tectum (9). As vertebrates evolved, the single system differentiated; two new centers developed at the targets of two separate pathways, the tectopulvinar path and the geniculo-striate path.

Raising these questions points to the main significance of the present line of inquiry: the prospect of determining how psychological functions become further specialized as the anatomical substrate differentiates and, eventually, of understanding the evolution of higher intellectual faculties.

H. KILLACKEY
I. T. DIAMOND
Department of Psychology, Duke University, Durham, North Carolina

### References and Notes

1. P. Abplanalp and W. Nauta, personal communication; ———, paper presented at the Conference on Subcortical Vision, Massachusetts Institute of Technology, Cambridge, June 1969 (*Brain Behav. Evolut.*, in press); I. T. Diamond, in *Contributions to Sensory Physiology*, W. D. Neff, Ed. (Academic Press, New York, 1967), vol. 2; ———, M. Snyder, H. Killackey, J. Jane, W. C. Hall, *J. Comp. Neurol.* 139, 273 (1970); M. Snyder, W. C. Hall, I. T. Diamond, *Psychonom. Sci.* 6, 243 (1966); M. Snyder and I. T. Diamond, *Brain Behav. Evolut.* 1, 244 (1968).
2. H. Killackey, M. Snyder, I. T. Diamond, *J. Comp. Physiol. Psychol.*, in press.
3. N. J. MacKintosh, in *Animal Discrimination Learning*, R. M. Gilbert and N. S. Sutherland, Eds. (Academic Press, London, 1969), chap. 7, part 2.
4. For a detailed description of the characteristics of these filters, see M. Snyder, H. Killackey, I. T. Diamond, *J. Neurophysiol.* 32, 554 (1969).
5. G. G. Simpson, *Bull. Amer. Mus. Natur. Hist.* 85, 1 (1945); W. E. Le Gros Clark, *The Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959); J. A. Jane, C. B. G. Campbell, D. Yashon, *Science* 147, 153 (1965); M. C. McKenna, *Folia Primatol.* 4, 1 (1966); L. Van Valen, *Evolution* 19, 137 (1965); A. S. Romer, *Science* 158, 1629 (1967).
6. C. M. Butter, M. Mishkin, H. E. Rosvold, in *Stimulus Generalization*, D. I. Mostotsky, Ed. (Stanford Univ. Press, Stanford, 1965).
7. L. A. Rothblat and W. A. Wilson, Jr., *Psychonom. Sci.* 17, 149 (1969).
8. E. Iwai and M. Mishkin, *Exp. Neurol.* 25, 585 (1969); M. Mishkin, in *The Brain and Human Behavior*, A. G. Karczmar, Ed. (Springer-Verlag, New York, in press).
9. I. T. Diamond and W. C. Hall, *Science* 164, 251 (1969).
10. Supported by National Institute of Mental Health grant 4849.

8 September 1970  ■

# Taste of Water in the Cat: Effects on Sucrose Preference

Abstract. *Electrophysiological recordings show that water is not tasteless to cats. Also, unlike most mammals, cats appear indifferent to sucrose, but this may be because the taste of the sucrose is masked by the taste of the water in which it is dissolved. When the water taste is suppressed by the addition of small amounts of sodium chloride, cats take sucrose avidly.*

Cross-species investigations led Zotterman and his co-workers to conclude that cats, dogs, monkeys, and pigs have taste fibers responsive to water, but rats and men do not (1, 2). This conclusion was later revised on the discovery that responses to water in squirrel monkeys, cats, rats, and hamsters (3, 4) are contingent on the preceding adapting stimulus: fibers respond to water-after-NaCl, or water-after-sucrose, or the like, but not to water per se. Responses to water occur in every species tested, although the optimal contingencies differ from species to species. In man, water tastes sweet after quinine hydrochloride (QHCl) and citric acid, salty after urea, and bitter after sucrose and NaCl. The saliva of some individuals contains enough NaCl in itself to make water taste bitter (5). The experiment reported here demonstrates an unusual effect of the taste of water: water can prevent a preference for sucrose, presumably through its ability to mask the taste of sucrose in the cat.

To the student of taste, sucrose is of special interest because it is accepted by so many animals including man, insects, pigeons, chickens, rats, rabbits, hamsters, cattle, and monkeys (6, 7). Are cats an exception to the general rule? Carpenter (7) found that they fail to discriminate between water and sucrose at any concentration up to 1.0M. In addition, in early electrophysiological studies no sucrose-sensitive fibers were found (8). Nevertheless Frings (9) observed that cats find sucrose (0.5M) highly acceptable when dissolved in milk rather than water. The study reported here resolves this apparent discrepancy. Cats do have some fibers sensitive to·sucrose (3, 10), but they also have water sensitive fibers that under normal salivary conditions may mask the sucrose responses and thereby interfere with taste discrimination. It is possible, however, to suppress the water responses and thereby render sucrose highly acceptable.

The idea that the water response is suppressible grew out of a study of neural responses from 26 single fibers obtained from 12 cats. The animal was anesthetized with sodium pentobarbital, and the chorda tympani taste nerve was surgically exposed and cut centrally. Action potentials from small groups of fibers separated from the whole nerve were recorded with a silver–silver chloride wick electrode,
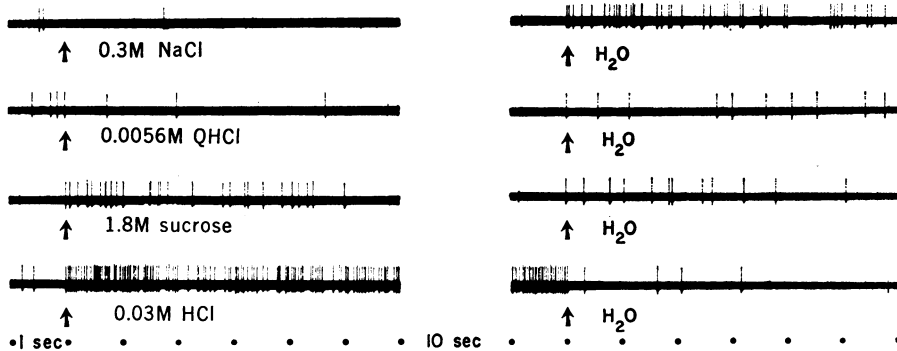
Fig. 1. Electrophysiological responses of a single fiber of the cat chorda tympani. Stimuli were applied in the order shown from left to right and top to bottom. The first 6 seconds of response following the onset of the stimulus (designated by arrows) are shown for each stimulus.

amplified, and photographed. Uniform spike height was the criterion for a single fiber. Each of the 26 fibers was tested for sensitivity to 0.3$M$ NaCl, 0.0056$M$ QHCl, 1.8$M$ sucrose, 0.03$M$ HCl, and to water that was applied immediately after each of these four solutions.

Figure 1 shows the responses of one fiber. Under a response criterion of an increase of five spikes or more in the first second, 5 fibers responded to NaCl, 13 to QHCl, 15 to HCl, and 7 to sucrose. In addition, 21 of the 26 fibers responded to water after one or more of the adapting solutions: 6 fibers responded to water-after-NaCl, 6 to water-after-QHCl, 14 to water-after-HCl, and 7 to water-after-sucrose (11). The "water" responses of the cat de-

scribed by Zotterman and his co-workers (1, 2) more properly might be called water-after-NaCl responses since their rinse was Ringer solution (containing about 0.15$M$ NaCl). Even though the water-after-NaCl response is only one of those recorded in the cat, it is particularly important in the present study because NaCl is a major constituent of saliva. When the cat drinks water, the NaCl in the cat's own saliva is an adapting stimulus, and the fibers sensitive to water-after-NaCl respond. When the cat drinks sucrose, both the fibers sensitive to water-after-NaCl and the fibers sensitive to sucrose respond. Most fibers that respond to water-after-NaCl will not respond to NaCl (12) (see also Fig. 1). This observation suggests that the water taste

in a sucrose solution can be suppressed by the addition of the right amount of NaCl. This amount depends on the adapting concentration (that is, saliva). Fibers sensitive to NaCl fire to concentrations higher than the adapting concentration, whereas fibers sensitive to water-after-NaCl fire to concentrations lower than the adapting concentration. The electrophysiological data suggest that 0.03$M$ NaCl suppresses water responses without stimulating NaCl responses, given any of a wide range of possible adapting concentrations (3).

Nine adult cats were tested in each of two preference experiments. The first experiment tested sucrose in water versus water; the second tested sucrose in 0.03$M$ NaCl versus 0.03$M$ NaCl. Tap water (13) was used to replicate Carpenter's experiment (7), but distilled water (13) was also used in control experiments. Each animal's cage had two glass tubes that allowed the cat to lap solutions from a small opening. The experimental design was essentially that of Carpenter: sucrose concentrations were presented in order of increasing concentration, and position preferences were controlled by counterbalancing. On a given day intake was limited to 200 ml or the amount consumed in 6 hours, whichever occurred first, and test days (four for each concentration) were separated by rest days. [Cats are relatively deficient in sucrase (14) and therefore are prone to severe diarrhea from continued sucrose ingestion.]

Figure 2A shows that the cats ingested nearly equal amounts of water and sucrose solution at every concentration tested. (That the two curves rise as a function of sucrose concentration is probably due to loss of liquid from slight diarrhea caused by the accidental intake of sucrose.) A very different picture emerges (Fig. 2B) when weak NaCl solution is used as the solvent instead of water; in these cases the animals strongly prefer the sucrose to the weak NaCl solution. A Friedman analysis of variance (15) showed that the differences shown in Fig. 2B were significant ($P < .01$) whereas those shown in Fig. 2A were not ($P > .8$). Control experiments showed that distilled water produced the same results as tap water and that water and 0.03$M$ NaCl were about equally acceptable in themselves.

The intake of the highest concentration of sucrose (0.375$M$) in NaCl
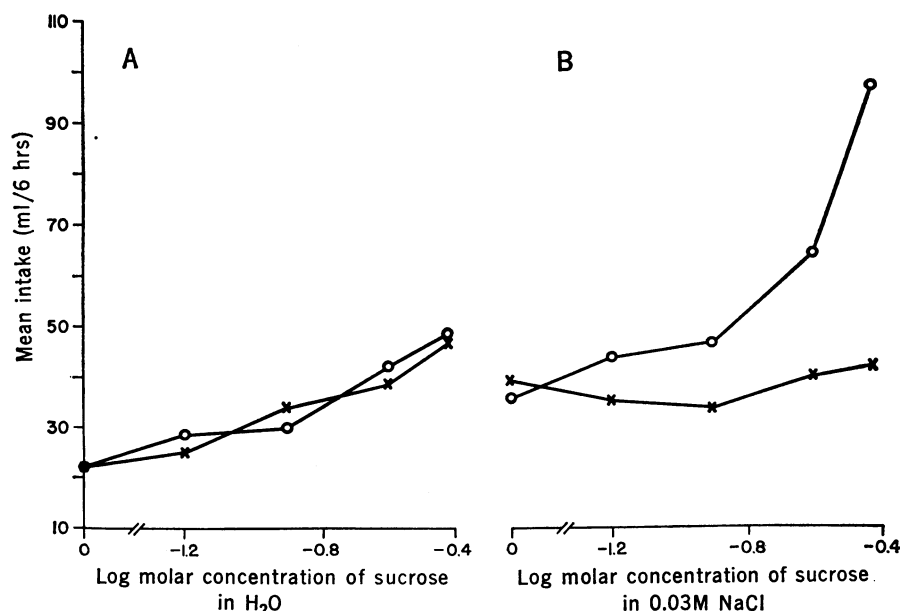


Fig. 2. Intake of sucrose dissolved in two different solvents as compared with the intake of the solvent alone. (A) Water as solvent; (B) 0.03$M$ NaCl as solvent. ○, Sucrose; X, solvent.

solution is shown for day 1 only (*16*), because, even though the intake was relatively small (mean intake, 98 ml), the cats became ill. Two drank sucrose almost continuously up to the criterion and subsequently vomited and developed diarrhea. The others did not vomit but developed diarrhea. The illness apparently led to conditioned aversion. After a week's rest, cats rejected 0.375*M* sucrose (mean intake, 18 ml). This same thing happened with 0.5*M* sucrose solution and 24-hour intake.

Frings's (*9*) finding that sucrose in dilute milk (one part milk to four parts water) is preferred by cats fits in well with the result presented here. Mean sodium and chlorine content for whole milk so diluted would approximate 0.006*M* NaCl (*17*). The exact whole-mouth salivary NaCl concentration for the cat is not known, but it must fall between 0.01*M* and 0.16*M* NaCl (*18*). For adapting concentrations in this range, electrophysiological data (*3*) suggest that the 0.006*M* NaCl in the milk used by Frings would at least partially suppress the water-after-NaCl response.

The taste of water has been widely ignored in behavioral testing. It is now clear that water should be regarded not as a neutral solvent but rather as a taste stimulus itself. The implications for receptor mechanisms are still unclear. Water appears to produce some responses by removing other stimuli (*2*), but it may also stimulate receptors directly [see (*19*) for a review of various structural models of water]. Nevertheless, electrophysiological studies can suggest how water tastes can be manipulated to assess the taste of any given substance in water.

L. M. BARTOSHUK
*John B. Pierce Foundation Laboratory,*
*290 Congress Avenue,*
*New Haven, Connecticut 06519*
M. A. HARNED
L. H. PARKS
*Pioneering Research Laboratory,*
*U.S. Army Natick Laboratories,*
*Natick, Massachusetts 01760*

**References and Notes**

1. G. Liljestrand and Y. Zotterman, *Acta Physiol. Scand.* **32**, 291 (1954); Y. Zotterman, *ibid.* **37**, 60 (1956); ———— and H. Diamant, *Nature* **183**, 191 (1959).
2. M. J. Cohen, S. Hagiwara, Y. Zotterman, *Acta Physiol. Scand.* **33**, 316 (1955).
3. L. M. Bartoshuk, thesis, Brown University (1965).
4. ———— and C. Pfaffmann, *Fed. Proc.* **24**, 207 (1965); C. Pfaffmann, in *Olfaction and Taste* C. Pfaffmann, Ed. (Rockefeller Univ. Press, New York, 1969), vol. 3, p. 528.

5. L. M. Bartoshuk, D. H. McBurney, C. Pfaffmann, *Science* **143**, 967 (1964); L. M. Bartoshuk, *Percept. Psychophys.* **3**, 69 (1968); D. H. McBurney, *J. Exp. Psychol.* **72**, 869 (1966); in *Olfaction and Taste*, C. Pfaffmann, Ed. (Rockefeller Univ. Press, New York, 1969), vol. 3, p. 407.
6. O. Maller and M. R. Kare, *Anim. Behav.* **15**, 8 (1967); V. G. Dethier and M. V. Rhoades, *J. Exp. Zool.* **126**, 177 (1954); C. Duncan, *Anim. Behav.* **8**, 54 (1960); H. L. Jacobs and M. L. Scott, *Poultry Sci.* **36**, 8 (1957); B. P. Halpern, *Amer. J. Physiol.* **203**, 541 (1962); M. R. Kare and M. S. Ficken, in *Olfaction and Taste*, Y. Zotterman, Ed. (Pergamon, New York, 1963), vol. 2, p. 285; J. Ganchrow and G. L. Fisher, *Psychol. Rep.* **22**, 503 (1968); C. Pfaffmann, *Amer. Psychol.* **20**, 21 (1965).
7. J. A. Carpenter, *J. Comp. Physiol. Psychol.* **49**, 139 (1956).
8. Y. Zotterman, *Skand. Archiv Physiol.* **72**, 73 (1935); C. Pfaffmann, *J. Cell. Comp. Physiol.* **17**, 243 (1941).
9. H. Frings, *Experientia* (*Basel*) **7**, 424 (1951).
10. C. Pfaffmann, *J. Neurophysiol.* **18**, 492 (1955).
11. The sensitivities to NaCl, QHCl, sucrose, and HCl appear to be independently associated in accordance with the random distribution hypothesis of M. Frank and C. Pfaffmann [*Science* **164**, 1183 (1969)]. In addition, the four contingencies producing water responses also appear to be independently associated in accordance with this hypothesis.
12. The correlation coefficient for water-after-NaCl responses and NaCl responses was −0.83 (*P* < .005). Only those fibers were included for which at least one response met the criterion. Previous reports of a negative correlation between water responses and NaCl responses [Cohen *et al.* (*2*); J. Nagaki, S. Yamashita, M. Sato, *Jap. J. Physiol.* **14**, 67 (1964)] probably reflect the negative correlation between water-after-NaCl and NaCl responses since the rinse was Ringer solution. The correlation coefficients for NaCl and water-after-QHCl, water-after-sucrose, and water-after-HCl are −0.65 (*P* < .05), −0.54 (*P* > .05), and −0.28 (*P* > .2), respectively.

13. We thank M. Dvorak and O. Stark of the Food Sciences Laboratory at the Natick Army Laboratories for analyses of the atomic absorption spectra of tap and distilled water samples. Samples were analyzed for Na, K, Ca, Mg, and halide. Tap water checked weekly for 2 months remained relatively constant with mean levels of $9.6 \times 10^{-4} M$ Na, $6.8 \times 10^{-5} M$ K, $7.1 \times 10^{-4} M$ Ca, $2.2 \times 10^{-4} M$ Mg, and $1.0 \times 10^{-3} M$ halide (predominantly Cl). Distilled water contained $8.7 \times 10^{-7} M$ Na, $5.1 \times 10^{-6} M$ K, $2.5 \times 10^{-6} M$ Ca, and $4.1 \times 10^{-7} M$ Mg.
14. P. Hore and M. Messer, *Comp. Biochem. Physiol.* **24**, 717 (1968).
15. S. Siegel, *Nonparametric Statistics* (McGraw-Hill, New York, 1956).
16. Since testing was discontinued after 1 day, the position of sucrose was not counterbalanced. To ensure that position preference could not account for the results at a sucrose concentration of 0.375*M*, position preference under all other conditions was tested with a two-tailed Walsh test (*15*). The results were not significant (*P* > .1).
17. K. Diem, Ed., *Scientific Tables* (Geigy Pharmaceuticals, Ardsley, N.Y., ed. 6, 1962), p. 516.
18. L. H. Schneyer and C. A. Schneyer, in *Handbook of Physiology: Alimentary Canal*, C. F. Code, Ed. (American Physiological Society, Washington, D.C., 1967), vol. 2.
19. O. Eisenberg and W. Kauzmann, *The Structure and Properties of Water* (Oxford Univ. Press, New York, 1969).
20. Electrophysiological data and preliminary behavioral data were obtained at Brown University where work was supported in part by a PHS predoctoral fellowship to L.M.B. and NSF grants G-14332 (to C. Pfaffmann) and GB-2754 (to C. Pfaffmann and L.M.B.). Final behavioral data were collected at the U.S. Army Natick Laboratories. We thank R. L. Gentile, J. C. Stevens, L. E. Marks, and W. S. Cain for valuable comments on the manuscript.

19 October 1970; revised 13 November 1970  ∎

# Mental Rotation of Three-Dimensional Objects

Abstract. *The time required to recognize that two perspective drawings portray objects of the same three-dimensional shape is found to be (i) a linearly increasing function of the angular difference in the portrayed orientations of the two objects and (ii) no shorter for differences corresponding simply to a rigid rotation of one of the two-dimensional drawings in its own picture plane than for differences corresponding to a rotation of the three-dimensional object in depth.*

Human subjects are often able to determine that two two-dimensional pictures portray objects of the same three-dimensional shape even though the objects are depicted in very different orientations. The experiment reported here was designed to measure the time that subjects require to determine such identity of shape as a function of the angular difference in the portrayed orientations of the two three-dimensional objects.

This angular difference was produced either by a rigid rotation of one of two identical pictures in its own picture plane or by a much more complex, nonrigid transformation, of one of the pictures, that corresponds to a (rigid) rotation of the three-dimensional object in depth.

This reaction time is found (i) to increase linearly with the angular difference in portrayed orientation and (ii) to be no longer for a rotation in depth than for a rotation merely in the picture plane. These findings appear to place rather severe constraints on possible explanations of how subjects go about determining identity of shape of differently oriented objects. They are, however, consistent with an explanation suggested by the subjects themselves. Although introspective reports must be interpreted with caution, all subjects claimed (i) that to make the required comparison they first had to imagine one object as rotated into the same orientation as the other and that they could carry out this "mental rotation" at no greater than a certain limiting rate; and (ii) that, since they perceived the two-dimensional pictures as objects