preference structure and a deficiency in modulation of preferential reactions by the retardates. The use of numerals in estimation of magnitude, however, does not offer an immediate explanation. The median number of numerals used by the retardates for the 30 excerpts is 15 (*Q*, 6.1) for the men and 10 (*Q*, 4.1) for the women; for the normals, 11 to 12 (*Q*'s, 1.3 to 2.4). Since the various number concepts (such as equalization and seriation) of the retardates include a mixture of Piaget's first three developmental stages (*6*), the large variability of our retardates in the use of numerals may reflect the heterogeneity of these intellectual processes. This measure, however, does not correlate with the mental age or internal consistency. Although only few retardates seem to reach Piaget's stage of abstract operation, clearly they can express meaningfully and consistently their musical preferences by means of numerals.

SOON DUK KOH
Research Section, Hastings State Hospital, Hastings, Minnesota
TONG-HE KOH
Faribault State School and *Hospital, Faribault, Minnesota*

References and Notes

1. S. D. Koh, *J. Exp. Psychol.* **70**, 79 (1965).
2. S. S. Stevens, *Psychol. Bull.* **54**, 177 (1958).
3. ———, *Psychol. Rev.* **64**, 153 (1957).
4. ———, *ibid.*, p. 153 (1957); G. Ekman and L. Sjöberg, in *Annual Review of Psychology*, P. R. Farnsworth, Ed. (Annual Reviews, Palo Alto, Calif., 1965), vol. 16, 451–74.
5. F. Attneave, *Applications of Information Theory to Psychology* (Holt, New York, 1959); W. R. Garner, *Uncertainty and Structure as Psychological Concepts* (Wiley, New York, 1962).
6. J. Piaget, *The Child's Conception of Number* (Routledge, London, 1952); M. Woodward, *J. Child Psychol. Psychiat.* **2**, 249 (1961).
7. Supported by NIH grant 10094. We thank G. Shears and D. Medalen for helpful suggestions.

7 April 1966

Stimulus Control in Pigeons Based on Proprioceptive Stimuli from Floor Inclination

Abstract. *Two groups of pigeons trained to peck a dimly illuminated disc in an otherwise dark experimental chamber with the floor horizontal (0° tilt) or inclined 30° to the left, respectively, show decremental generalization gradients of response rate when the floor inclination is varied from its training position. Discrimination training in which food reinforcement is available under one floor tilt condition but not under another steepens the slope of such gradients. In a second experiment, pigeons reinforced for pecking when the floor was tilted 10° or 20° and not reinforced under the alternative condition showed steep gradients with maximal responding displaced from the reinforced stimulus.*

Proprioceptive feedback is widely assumed to play a significant role in mediating many types of learned behavior. Hull (*1*) posited proprioceptive stimulation as vital to serial learning. Hefferline (*2*) has shown that proprioceptive feedback can function as a source of discriminative stimuli. More recently, attention has focused on the relative contribution of proprio- and exteroceptive stimuli in controlling behavior in the free operant situation. Hearst *et al.* (*3*), Blough (*4*), and Thomas and Switalski (*5*) have suggested that flatter stimulus generalization gradients along an exteroceptive dimension result when reinforcement schedules are used in which response-generated stimulation becomes a discriminative stimulus for further responding. Presumably, internal and external stimuli compete for the control of responding, and thus schedules which emphasize the significance of response-produced stimulation necessarily do so at the cost of reduced external stimulus control.

The use of different reinforcement schedules is one way of manipulating proprioceptive stimulation. An alternative procedure for investigating stimulus control by proprioceptive feedback is to produce postural adjustments by changing the inclination of the floor on which the animal stands and observing subsequent changes in behavior. By training birds to respond in a dark chamber when the floor is inclined a specified degree, and then testing under other positions of tilt, it should be possible to measure the control gained by these postural cues alone.

The apparatus consisted of a standard Grason-Stadler pigeon chamber, except that the floor, a refrigerator shelf covered with ½-inch (1¼-cm) hardware cloth, was mounted on a shaft running lengthwise through the midline of the chamber from the rear wall to the front panel, on which the pecking disc and feeder were mounted. An external gear arrangement permitted the floor to be smoothly rotated into any angle of inclination between 0° and 30° in either direction from horizontal. In the first experiment, only changes in one direction were used, that is, the left side lowered (and right raised) the specified angular distance from horizontal.

Seventeen experimentally naive homing pigeons were trained to peck an illuminated disc in an otherwise completely dark chamber for variable-interval reinforcement with a mean inter-reinforcement period of 2 minutes (V.I.–120 seconds). For eight of these birds the floor of the chamber was always inclined 30° to the left, while for the other nine the floor was in the typical horizontal position. Initial magazine training and response-shaping took place on the designated floor tilt. Daily training sessions were approximately 30 minutes in duration. After approximately 13 days of V.I.–120 seconds training, time-out periods were introduced during which the chamber was in complete darkness and reinforcement was not available (*6*). Time-out periods of 60 seconds were randomly alternated with stimulus presentation periods of 60 seconds. During the periods of stimulus presentation the same V.I.–120 seconds schedule remained in effect. After 3 days of time-out training, the subjects were tested in extinction for generalization to floor inclinations of 0°, 10°, 20°, and 30°. After a 5-minute warm-up period under the original training condition, these four stimuli were randomized in a series, and 12 different random series were presented to each subject. Stimulus presentation periods were for 60 seconds with intervening 15-second time-out periods. These time-out periods permitted the experimenter to record responses and to adjust the floor inclination for the next test period, while allowing subjects time to recover from possible emotional and vestibular effects of the movement of the floor.

After the stimulus generalization test, the subjects were given discrimination training with the previous conditioned stimulus as the positive stimulus (S+) and the alternative condition (0° or 30°) as the negative stimulus (S−). In daily training sessions each floor position was presented 15 times for 1-

minute intervals, in a random order, with a 15-second time-out period intervening between presentations. Responding during S+ was reinforced on a V.I.–30 seconds schedule until a criterion of responding 10 : 1 (S+ : S−) was met on two successive days. The schedule was then changed to V.I.–120 seconds, and after two more consecutive days of criterion responding, another generalization test similar to that reported earlier was administered. Meeting this criterion required a median of 21 days (range, 9 to 32 days).

Stimulus generalization gradients on each test were determined for each subject in terms of percentage of total responses made to each of the four test positions. The group means of these gradients under both training conditions on both tests are presented in Fig. 1. The test 1 data reveal that changing the floor position away from the training position reduces the rate of responding. The gradient obtained is significant (that is, response percentages differ significantly according to an analysis of variance), regardless of whether 0° or 30° was the conditioned stimulus ($p < .01$ and $p < .025$, respectively) (*7*). During the course of generalization testing, the gradients of both groups of pigeons became steeper. This effect has been reported for the wavelength dimension (*8*) and it argues against an interpretation of the gradient in terms of the novelty of the test stimuli.

The test 2 data indicate that discrimination training results in a markedly steepened generalization gradient. All subjects in the experiment generated a steeper generalization gradient on test 2 than on test 1, that is, a higher percentage of total responses was emitted to the S+ value. That the subjects can in fact distinguish a 10° difference in tilt of the floor is indicated by the differential response percentages now obtained at all values on test 2.

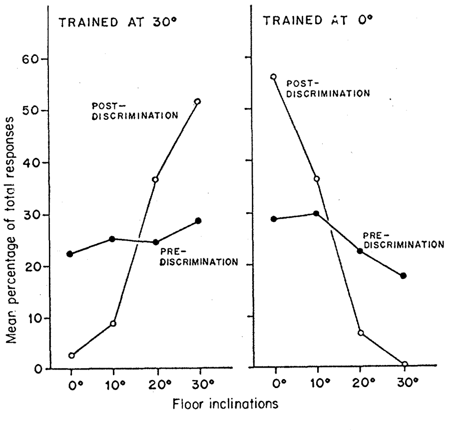

Fig. 1. Mean stimulus generalization gradients prior to and after discrimination training in the first experiment.

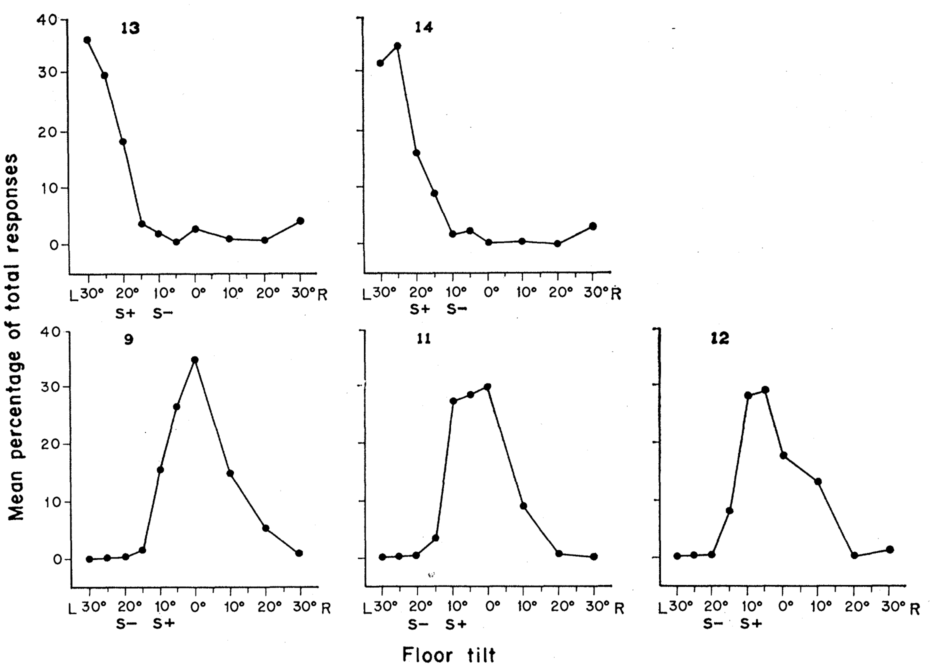

Fig. 2. Individual stimulus generalization gradients after discrimination training in the second experiment.

Two effects of successive intradimensional discrimination training have commonly been reported in the literature, a steepening of the gradient and a displacement of the peak (mode) of responding from the S+ in a direction away from the S− (*9*). In the first experiment only the former effect could be observed, since the generalization test was restricted to values between S+ and S−. For this reason, a second experiment was performed, in which five experimentally naive homing pigeons were trained to discriminate between floor tilts of 10° left and 20° left, in the same apparatus and with the same procedure employed in the discrimination training phase of the first experiment. For three of the subjects, 10° was S+, 20° S−; for two, the reverse. Meeting the 10 : 1 (S+ : S−) criterion required a median of 33 days (range, 31 to 39 days). The generalization test included all values from 30° left to 30° right in 5° steps, randomized within a series, with five different series administered during the test. As in the first experiment, stimulus presentations were for 60 seconds with 15-second time-out periods intervening. The results in every case, as shown in Fig. 2, are steep gradients with the mode of responding displaced from S+ in the direction opposite S−.

These two experiments provide evidence that stimulus control can indeed be achieved through proprioceptive feedback from floor inclination (*10*). Such feedback does not merely provide a discriminative cue for operant responding, but rather constitutes a stimulus dimension along which experimental manipulations affect responding in the same manner as they do along exteroceptive dimensions such as wavelength and auditory frequency.

DAVID C. RICCIO
MICHAEL URDA
DAVID R. THOMAS
Kent State University,
Kent, Ohio 44240

References and Notes

1. C. L. Hull, *A Behavior System* (Yale Univ. Press, New Haven, 1952).
2. R. F. Hefferline, in *Experimental Foundations of Clinical Psychology*, A. J. Bachrach, Ed. (Basic Books, New York, 1962), chap. 4.
3. E. Hearst, M. B. Koresko, R. Poppen, *J. Exp. Anal. Behav.* **7**, 369 (1964).
4. D. Blough, in *Stimulus Generalization*, D. I. Mostofsky, Ed. (Stanford Univ. Press, Stanford, Calif., 1965), chap. 3.
5. D. R. Thomas and R. W. Switalski, *J. Exp. Psychol.* **71**, 236 (1966).
6. On the tenth day of training the birds received a wavelength generalization test as part of another experiment.
7. For birds trained on 30° floor tilt: $F = 3.49$, $df = 3/45$, $p < .025$; for birds trained on 0° tilt: $F = 12.89$, $df = 3/45$, $p < .01$. For both groups combined: $F = 13.83$, $df = 3/45$, $p < .001$; for the interaction: $F = 2.55$, $df = 3.45$, $p > .05$.
8. H. Friedman and N. Guttman, in *Stimulus Generalization*, D. I. Mostofsky, Ed. (Stan-

ford Univ. Press, Stanford, Calif., 1965), chap. 17; D. R. Thomas and E. Barker, *Psychonomic Sci.* **1**, 119 (1964).
9. H. M. Hanson, *J. Exp. Psychol.* **58**, 321 (1959); W. K. Honig, D. R. Thomas, N. Guttman, *ibid.*, p. 145; D. R. Thomas, *ibid.* **64**, 24 (1962).
10. As commonly employed, the term "proprioception" refers to kinesthetic stimulation emanating from the muscles and joints and sensations from the vestibular system [see F. Geldard, *The Human Senses* (Wiley, New York, 1953), p. 233]. Observations of the pigeons standing on the tilted floor indicated that their heads were maintained in an upright position, suggesting that the kinesthetic receptors are the major mediating system operative in this experimental situation.
11. Supported in part by NIH research grant RO 1-HD-00903-05, under the direction of D.R.T. Norma Haggberg, John Erdner, Richard Davis, and David Centa aided in the collection of the data. A paper based on this study was read by D.R.T. at the May 1966 meetings of the Midwestern Psychological Association in Chicago, Ill.

12 May 1966

Taxonomic Status of Tree Shrews

The report by A. S. Hafleigh and C. A. Williams, Jr. (*1*) again raises the question of the taxonomic status of the tree shrews. A comment on their findings and on those of other recent studies seems appropriate. Van Valen (*2*) has reexamined the evidence, with the exception of the neuroanatomical evidence, which has been thought to indicate a primate status for the Tupaiidae and has added some from his own studies. He concluded that ". . . a special tupaiid-primate relationship is possible but unlikely and that the similarities between Recent tupaiids and primates are probably convergences and primitive retentions." McKenna (*3*), after examining much of the anatomical evidence, concluded that the tupaiids should be regarded as leptictid-like insectivores, and that among living nonprimates the tupaiids are the closest primate relatives.

I have reexamined the neuroanatomical evidence (*4*). With the exception of relative brain size, all of the characteristics cited by Le Gros Clark (*5*) may be directly related to the fact that tupaiids, other than *Ptilocercus*, have an elaborate visual system. Tree shrews, other than the nocturnal *Ptilocercus*, are diurnal animals adapted to an arboreal or scansorial way of life. Many of the characteristics listed by Le Gros Clark as indicative of primate affinity, such as presence of a calcarine sulcus, advanced development of certain elements of the thalamus, and downward displacement of the rhinal sulcus, are found in an arboreal, nocturnal marsupial, *Trichosurus vulpecula* (*6*). A great deal of emphasis has been placed on the presence in the tree shrew of a laminated, dorsal lateral geniculate nucleus. Laminated, dorsal lateral geniculate nuclei are found in all primates. They are also found in some nonprimates, including *Trichosurus vulpecula.* Three separate studies (*7*) reveal that in *Tupaia glis* uncrossed fibers from the retina terminate in the innermost and outermost laminae of the ipsilateral nucleus (laminae 1 and 5), while crossed fibers terminate chiefly in laminae 2 and 4 (with a somewhat less pronounced projection to laminae 3) in the contralateral dorsal lateral geniculate nucleus. This is the direct opposite of the situation found in every primate which has been examined (*5*). This strongly suggests to me that the elaborate visual system on which many of the arguments for a primate status for the tree shrews have been based is a result of convergent evolution.

The fact that *Tupaia* has serum albumin more like that of primates than that of insectivores such as the hedgehog, as reported by Hafleigh and Williams, is not a new finding. Goodman (*8*) has already reported this finding and has given the same possible explanation for it as that suggested by Hafleigh and Williams. However, he also reported that with antisera to hedgehog and tree shrew sera, hedgehog and tree shrew sera showed more correspondence to each other than to any of the other nonprimates and primates tested. When the cross reactions of the lower primates and nonprimates with antisera to human serum proteins other than albumin (gamma globulin and alpha$_2$ macroglobulin) were tested, the lemur and galago developed larger cross reactions than did the tree shrew and nonprimate mammals. The major genera of primates, including anthropoids and prosimians, but excepting the tree shrew, *Tupaia glis*, accept passive sensitization by human atopic reagins whereas none of the nonprimates do (*9*).

Much has been made of the fact that tree shrews supposedly possess a hemochorial placenta similar to the anthropoid primates (*10*). Hill (*11*) has shown that several species of Tupaia have an endotheliochorial placenta unlike that of any primate.

The relationships of various primates and nonprimates to man have been examined in a study of the homologies of their polynucleotide sequences (*12*). In this study, the competition of unlabeled DNA fragments from various primate and nonprimate sources was examined. Human DNA labeled with C^{14} and unlabeled human DNA embedded in agar was the indicating system. It was determined that anthropoid ape DNA fragments competed 94 to 100 percent with the labeled human DNA; New and Old World monkey fragments, 83 to 88 percent; and prosimian fragments, 47 to 65 percent. The competition of DNA from tree shrews was only 28 percent as compared to that from the African hedgehog which was 19 percent and that from the mouse which was 21 percent. This data essentially agrees with the generally accepted views on primate relationships.

I have attempted to indicate the large number of recent studies whose results indicate that a close relationship between tupaiids and primates is unlikely. The finding mentioned by Hafleigh and Williams and previously discovered by Goodman is inconsistent with the bulk of recent evidence. There is no doubt that the inclusion of the tree shrew as the most primitive primate in the morphological sequence: tree shrew - lemur - tarsier - ape - man is an attractive picture. Its innate attractiveness may have been in large measure responsible for its acceptance.

C. B. G. Campbell
Department of Neurophysiology,
Walter Reed Army Institute of
Research, Washington, D.C. 20012

References and Notes

1. A. S. Hafleigh and C. A. Williams, Jr., *Science* **151**, 1530 (1966).
2. L. Van Valen, *Evolution* **19**, 137 (1965).
3. M. McKenna, *Folia Primatologica* **4**, 1 (1966).
4. C. B. G. Campbell, *Evolution*, in press.
5. W. E. Le Gros Clark, *The Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959).
6. F. Goldby, *J. Anat.* **75**, 197 (1941); A. D. Packer, *ibid.* **75**, 309 (1941); personal observations.
7. J. Tigges, *Folia Primatologica* **4**, 103 (1966); C. B. G. Campbell, J. A. Jane, D. Yashon, *Anat. Rec.* **154**, 348 (1966); M. Glickstein, W. Calvin, R. W. Doty, *ibid.* **154**, 348 (1966).
8. M. Goodman, in *Classification and Human Evolution*, W. L. Washburn, Ed. (Aldine, Chicago, 1963).
9. L. Layton, *J. Allergy* **36**, 523 (1965).
10. W. Meister and D. D. Davis, *Fieldiana: Zool.* **35**, 73 (1956).
11. J. P. Hill, *J. Zool.* **146**, 278 (1965).
12. B. H. Hoyer, E. T. Bolton, M. Goodman, in preparation.
13. B. H. Hoyer, B. J. McCarthy, E. T. Bolton, *Science* **144**, 959 (1964).

6 May 1966