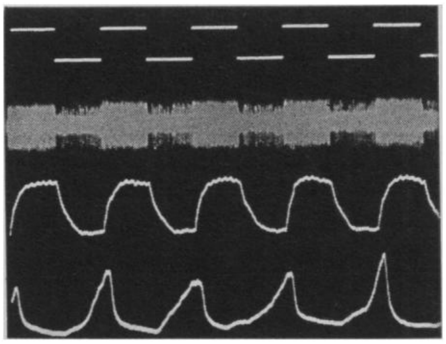

Fig. 2. Pretectal unit correlating with constriction. Same display as in Fig. 1. Time for all traces and stimulus amplitude can be calibrated by noting that the light stimulus changes from 0.001 to 1 mlu/m^2 for 2.5 seconds every 5 seconds. The fourth trace can be calibrated as above by noting that the last response changes from a dilated base line (really a peak) of 17 mm^2 to a constriction level of 10 mm^2.

light stimulation. The contralateral or ouptut eye was illuminated with infrared light, and a photodiode was positioned 1 cm in front of the responding pupil. The photodiode responded sensitively to variations in reflected infrared light from the iris of the output eye (*3*), and the resultant signal in pupil area was then amplified with a d-c coupled device. Electrodes of insulated (Insl-X) tungsten wire were used for extracellular recording (*4*). The electrode path was determined stereotaxically with the result that both neural and pupillary records were taken from the same side of the animal. The electrodes were advanced by means of a hydraulic system, and recording sites were coagulated with direct current. With the aid of histological verification, stimulation and recording sites were determined for 32 units in the pretectal area and for 41 units in the anterior oculomotor nucleus and oculomotor tract. Records of light flux input, pupil area, and single-unit activity were recorded on a tape recorder and on the digital computer for subsequent analysis.

Our results demonstrate that oculomotor units in the cat generate spike trains which, when integrated on a simple lag circuit, correlate with the light-driven response in pupil area and with the noise of the pupil area (noise denotes all pupil fluctuations not driven by the light stimulus). The activities of these midbrain neurons correlate with either pupillary dilatation (firing rate increases as pupil area increases) or with pupillary constriction (firing rate increases as pupil area decreases). The iris-muscle response of the pupil occurred after the nerve train with a delay of approximately 200 msecs; and direct stimulation of ciliary nerve endings also show this 200-msec delay for iris muscle (*5*). Figure 1 shows the unit activity recorded from the oculomotor nucleus. These units exhibited fairly regular spontaneous activity ranging from 8 to 20 pulse/sec. A total of eight dilatation-correlated oculomotor units were found. In three of the units found, the area adjacent to the unit was investigated by focal electrical stimulation with the same recording electrode being used. Pupil responses to electrical pulse trains (30 pulse/sec, 2 μa) were always the same as that seen during high firing rates of the particular unit during stimulation with light. Sometimes focal stimulation of the oculomotor area resulted in constriction of the pupil; no data on single units was obtained with the results of this type of stimulation. Only two questionable single units for constriction were observed at all.

Most single-unit activity recorded from the pretectal area exhibited a response pattern similar to those of the optic nerve and lateral geniculate body, namely, "on" (nine units), "off" (five units), and "on-off" (12 units) (*6*). Figure 2 shows the activity of such a unit correlated with the constriction phase of the recorded response of the pupil area.

Almost all units in the pretectal area responded to light; however, spontaneous activity from many units in the oculomotor region (approximately 31) did not appear to correlate with either the light stimulus or pupil area. These units characteristically maintained regular spontaneous activity; it is possible that they are associated with the lens accommodation system, the nictitating membrane, or even with extraocular motor neurons, all of which would presumably have no direct sensory input from the visual pathway.

JAMES D. SMITH
LESTER Y. ICHINOSE
GERALD A. MASEK
TAKESHI WATANABE*
LAWRENCE STARK†
Department of Biomedical Engineering, Presbyterian-St. Luke's Hospital, and
College of Engineering, University of Illinois, Chicago Circle, Chicago 60680

References and Notes

1. I. Nisida and H. Okada, *Jap. J. Physiol.* **10**, 64 (1960).
2. J. Terdiman, J. D. Smith, L. Stark, in preparation.
3. L. Stark, *Proc. Inst. Radio Eng.* **47**, 11 (1959).
4. D. H. Hubel, *Science* **125**, 549 (1957).
5. B. L. Dennison, personal communication.
6. I. Nisida, H. Okada, O. Nakano, *Yonago Acta Med.* **4**, 7 (1959).

7. Partially supported by the W. Clement and Jesse V. Stone Foundation, NIH grants NB-07803, NB-06197, NB-06487; and GM-01436; PHS MH-8396, and ONR N-0014.

* On leave from Department of Physiology, Tokyo Medical and Dental University.

† Present address: Department of Physiological Optics, University of California, Berkeley.

20 August 1968; revised 9 October 1968

Discrimination Learning as the Summation of Excitation and Inhibition

Abstract. *Pigeons received either excitatory, inhibitory, or combined excitatory and inhibitory (intradimensional) training to discriminate line-tilt stimuli. Algebraic summation of relative-generalization gradients obtained after separate excitatory and inhibitory training sessions was used to predict characteristics of gradients after intradimensional training. The good agreement between obtained and predicted gradients provided support for gradient-interaction theory.*

After an organism learns to make a response to one value along a stimulus dimension and to withhold response to another stimulus value, the organism may then be tested with entirely new values in order to determine the stimulus properties which controlled performance on the original discrimination. Pavlov (*1*) discussed behavioral outcomes from such experiments in terms of two competing cortical processes, "excitation" produced by the association of reinforcement with the positive stimulus (S+) and "inhibition" produced by the association of nonreinforcement with the negative stimulus (S−). Pavlov's interpretation was vague and overspeculative in its accounts of brain function, but in 1937 Spence proposed a more specific and testable theory of discrimination learning by treating the concepts of excitation and inhibition in an essentially nonphysiological manner (*2*). This theory posited a summation of separate stimulus-generalization gradients of excitation

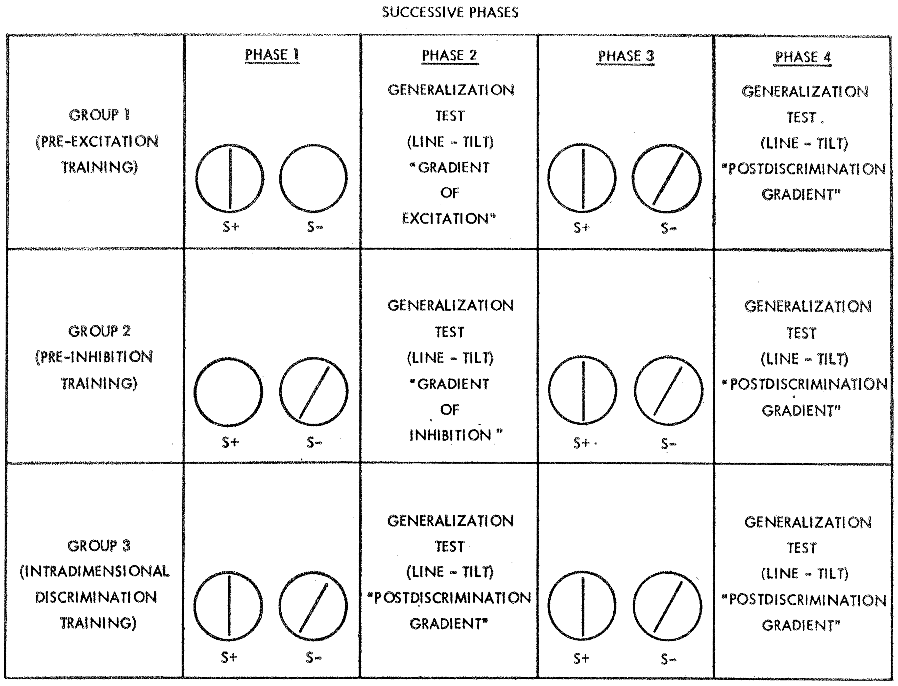

Fig. 1. The experimental paradigm for a case where the positive stimulus (S+) is a vertical line (0°), and the negative stimulus (S—) is a line tilted 30° clockwise (+30°) in the intradimensional discrimination.

and inhibition; two separate habits were said to interact, producing differential control of behavior by various new stimuli after training on an intradimensional discrimination.

Spence's theory handled the phenomenon of "transposition," which Gestalt psychologists had claimed was due to the learning of relations between stimuli rather than to the conditioning of separate habits to positive and negative stimuli (*3*). The basic logic and assumptions of Spence's approach were extended to other aspects of discrimination learning, for example, by Hull (*4*), and are still influential (*5*).

A major impediment to the development and precise evaluation of this type of theory has been the hypothetical or arbitrary nature of the postulated generalization gradients. Spence himself noted this weakness: "The selection of the curves of generalization has been more or less arbitrary, as little evidence bearing on the problem is available" (*2*). A variety of empirical methods for obtaining excitatory, inhibitory, and intradimensional gradients has since been developed, particularly by students of operant behavior (*6*). The experiments reported here combine some of these new techniques within a single paradigm permitting an experimental analysis of excitation and inhibition as well as a quantitative evaluation of some specific implications of the gradient-interaction approach.

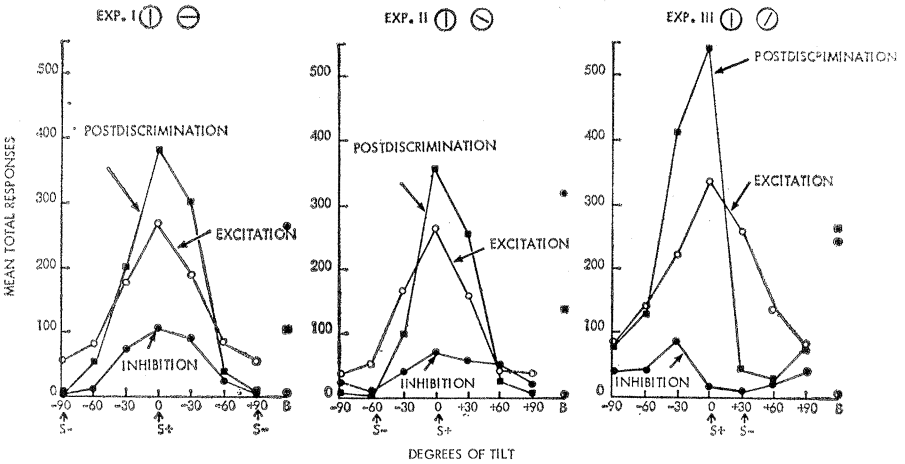

Fig. 2. Absolute group gradients of excitation, inhibition, and postintradimensional discrimination for three separate experiments differing in the distance between the line-tilts used as positive stimulus (S+) and negative stimulus (S—). The values for S+ and S— in each experiment are indicated by arrows on the abscissa. Data points above "B" at the extreme right of each set of gradients display the mean total responses to the blank stimulus throughout the entire generalization test.

This paradigm is illustrated in Fig. 1. Before phase 1, White Carneaux pigeons (seven to nine subjects in each group), maintained at 75 percent of their free-feeding weights, learned to peck a key for reinforcement with grain on a variable-interval schedule for seven 40-minute sessions (*7*). This preliminary phase provided a base line for later evaluation of contrast effects (*8*). The positive stimulus (S+ in phase 1 of Fig. 1) was present on the key during all stimulus-on periods, which lasted 30 seconds and were separated by 10-second blackouts throughout the entire experiment.

The only differences in treatment of the three groups in Fig. 1 occurred in phase 1. The birds in group 1 were trained on a successive discrimination in which they were rewarded on a 1-minute variable-interval schedule in the presence of a black vertical line (S+) on the white key and were given no reinforcement in the presence of a blank white key (S—); there was a mixed order of presentations of 30 positive and 30 negative stimuli in each 40-minute session. Thus, this group received excitatory training to a value on the line-tilt dimension. The birds in group 2 received variable-interval reinforcement in the presence of the blank key but were not rewarded in the presence of a line tilted 30° clockwise from the vertical axis; thus, this group received inhibitory training to a value on the line-tilt dimension. The birds in group 3 were given variable-interval reinforcement in the presence of a vertical line on the key (just as for group 1) but were not rewarded in the presence of a 30°-tilted line, just as for group 2; thus, group 3 received both excitatory and inhibitory training along the line-tilt dimension, unlike groups 1 and 2 which received either one or the other. Since the blank key is presumably orthogonal to values along the line-tilt dimension, training with the blank in groups 1 and 2 should not differentially affect responding to any specific values along that dimension.

Each subject remained on its respective phase 1 until it attained a predetermined criterion of discrimination; response rate in S– throughout a given session had to be less than 10 percent of response rate S+. On the day after reaching criterion, each bird received a test for generalization with no reinforcement possible. Six different line orientations (30° apart), and the blank key, were presented in each of 12 randomized blocks, and the total number of responses to each stimulus value was recorded. Thus, group 1 provided an excitatory line-tilt gradient around S+, group 2 provided an inhibitory line-tilt gradient around S–, and group 3 provided a line-tilt gradient which was presumably some combination of the two.

Phase 3 began on the next day. Birds in groups 1 and 2 received training to a 10 percent discrimination criterion on the intradimensional task that group 3 had already mastered in phase 1. Birds in group 3 continued on the same discrimination, for a time approximately yoked to the number of sessions required for the other groups to reach criterion. On the next day each subject was given another test for generalization (*9*).

As a test of gradient-interaction theory, the difference between S+ and S– was varied in three separate experiments. Because of the presumed greater overlap of excitatory and inhibitory gradients, a discrimination involving a small difference between S+ and S– should take longer to master than discriminations involving relatively large differences. The theory also predicts that marked shifts in distribution away from S– in gradients after intradimensional training should be most likely to occur when S+ and S– are close to each other (*10*). The line-tilt of the positive stimulus was always vertical (0°), but in different experiments S– was either ± 90° (horizontal), – 60° (a line tilted 60° counterclockwise), or + 30° (a line tilted 30° clockwise). Each of these three separate experiments followed the paradigm ilustrated in Fig. 1 for the experiment in which the angle was + 30°.

Birds in group 3 required a median of 4.0 days to reach criterion during phase 1 for either the 90° or 60° difference, but took 12.0 days when the difference between S+ and S– was small (30°). Thus the difficulty of the discrimination was inversely related to the physical difference between S+ and S–. A more critical test of gradient-interaction theory involves data from the generalization tests of phase 2, that are displayed in the form of absolute gradients in Fig. 2 for the three experiments.

As theory requires, all simple excitatory gradients showed maximum responding at positive stimulus, all simple inhibitory gradients showed minimum responding at the appropriate negative stimulus, and the postdiscrimination (intradimensional-training) gradients exhibited distribution shifts in the direction and relative amount predicted by theory. However, all postdiscrimination gradients showed higher absolute levels of response in the region of S+ than did the corresponding excitatory gradient; this effect was greatest in the experiment involving the small, 30° separation. These findings do not support the strict theory of Spence and Hull, who predicted an intradimensional gradient everywhere below the excitatory gradient, due to the weakening effect of inhibition all along the combined gradient. As Terrace and Reynolds pointed out (*6*, *8*), Spence and Hull did not consider the phenomenon of behavioral contrast during operant discrimination learning (that is, increased response strength to S+ during the acquisition of a discrimination), which invalidates their predictions about absolute response levels in this behavioral situation.

Nevertheless, the theory probably ought not to be evaluated in its strictest sense only. Perhaps measures of relative generalization that equate for absolute differences in the various gradients permit a clearer test of its major predictions. There is some suggestion (*11*) that behavioral contrast is not a stimulus-specific phenomenon, and thus its contaminating influence on absolute response levels might not be importantly reflected in relative scores.

The relative-generalization graphs of Fig. 3 display empirical relative excitatory and inhibitory gradients, with each value in Fig. 2 expressed as a percentage of the total responses on its respective gradient. The excitatory gradients in Fig. 3 combine data from all experiments, since the treatment was exactly the same in phases 1 and 2 for group 1 in the three experiments. The inhibitory gradients are displaced downward along the ordinate from their actual percentage values; minimum inhibition (maximum responding) in each group

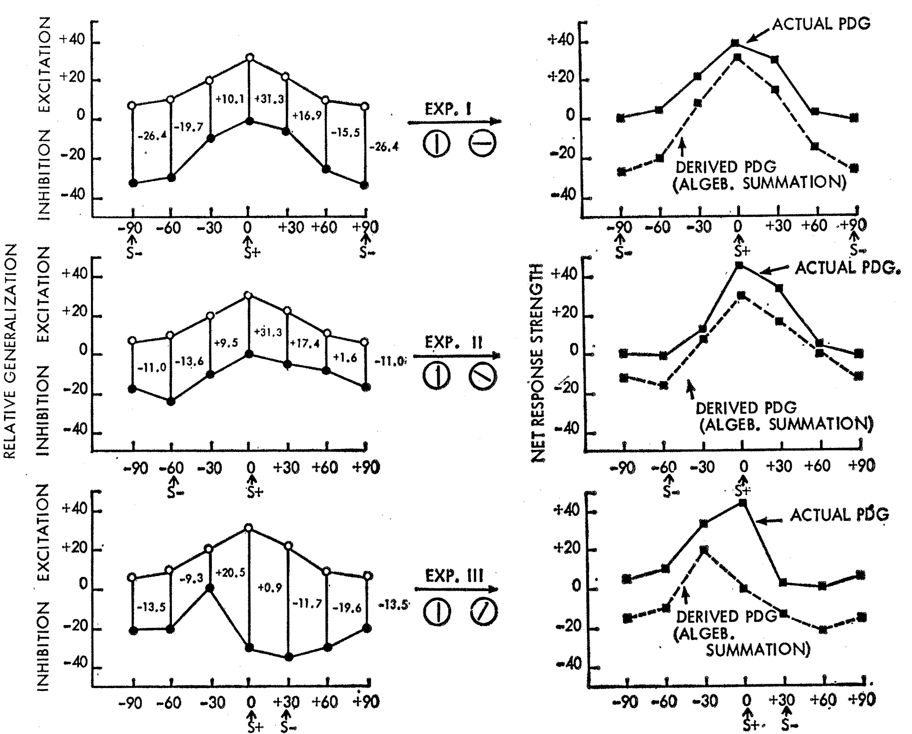

Fig. 3. (Left) Relative gradients of excitation (open circles) and inhibition (filled circles) calculated from the corresponding absolute data of Fig. 2. The numerical values alongside the vertical lines between each set of gradients represent the algebraic sum of the two points which the particular line connects. (Right) Actual (solid lines) postintradimensional discrimination gradients (PDG) of relative generalization, calculated from the corresponding absolute data of Fig. 2, compared with PDG (dashed lines) derived from the calculations of algebraic summation (above left).

2 was arbitrarily set at zero and other scores were plotted in a negative direction below zero. In similar fashion to Hull's treatment of hypothetical summation curves (*4*), these empirical excitatory and inhibitory gradients were algebraically summed, yielding the numerical values that are given in the left-hand graphs and plotted in the "derived" postdiscrimination gradients (PDG) on the right-hand side of Fig. 3.

The agreement between the shapes of the derived and actual relative PDG's was good for all three amounts of stimulus separation, with the exception of the discrepancy at S+ for the separation experiment of 30° (*12*). As a measure of the amount and direction of shift in distribution, the ratio of total scores on the right side of S+ to total scores on both sides of S+ was calculated for each actual and derived gradient. To avoid complications arising from negative values, a constant was added to every score in each derived gradient, so as to make the corresponding derived and actual gradients coincide at the minimum value in the actual gradient. These calculations revealed that there was only a minor shift to the right when S— was ± 90° (57.6 percent of the total scores were on the right side of the gradient for the actual PDG and 55.5 percent for the derived PDG, as compared to 50.9 percent for the excitatory gradient), a larger shift to the right when S— was −60° (73.1 percent lay on the right for the actual PDG and 64.7 percent for the derived PDG), and a very large shift to the left when S— stimulus was + 30° (19.3 percent lay on the right for the actual PDG and 24.2 percent for the derived PDG). The directions of these shifts and the rank orders of magnitudes of shifts in the three experiments were thus exactly the same for the actual and derived measures.

The above paradigm seems a promising framework for studying the empirical relations among excitatory, inhibitory, and intradimensional-discrimination gradients. Moreover, such gradients may replace the hypothetical or arbitrary ones often used to test gradient-interaction theories like that of Spence and Hull. The elegance and generality of this type of theory, which may be extended (*13*) to cover such phenomena as overtraining effects, errorless learning, peak-shift and stimulus-intensity dynamism, classical conditioning, and avoidance learning, seem sufficient reasons for justifying thorough empirical tests. Perhaps more sophisticated mathematical transformations of the obtained excitatory and inhibitory gradients, instead of the simple relative measures used in Fig. 3, would yield even more accurate predictions of differential stimulus control after intradimensional training (*14*). In any event, the gradient-interaction approach seems a valuable way to analyze intradimensional-discrimination learning, and this study indicates the feasibility of a direct attack on some of the assumptions and implications of this type of theory.

ELIOT HEARST*
Department of Psychology,
University of Missouri, Columbia

References and Notes

1. I. P. Pavlov, *Conditioned Reflexes* (Oxford Univ. Press, London, 1927).
2. K. W. Spence, *Psychol. Rev.* **44**, 430 (1937).
3. W. Kohler, *Gestalt Psychology* (Liveright, New York, 1929).
4. C. L. Hull, *A Behavior System* (Yale Univ. Press, New Haven, 1952), pp. 59–99.
5. D. A. Riley, *Discrimination Learning* (Allyn and Bacon, Boston, 1968).
6. H. S. Terrace, in *Operant Behavior: Areas of Research and Application*, W. K. Honig, Ed. (Appleton-Century-Crofts, New York, 1966), pp. 271–344.
7. An experimental chamber commercially produced by Lehigh Valley Electronics Co. was used. See E. Hearst, M. B. Koresko, R. Poppen [*J. Exp. Anal. Behav.* **7**, 369 (1964)], for relevant details concerning experimental method, apparatus, and equation of the brightnesses of the projected stimuli.
8. G. S. Reynolds, *ibid.* **4**, 289 (1961).
9. Space is not available in this report to discuss at length the data of phases 3 and 4. But in every experiment birds given preexcitation training in phase 1 (that is, group 1) learned the phase 3 discrimination more rapidly than birds given preinhibition training in phase 1 (that is, group 2). The same result has been obtained in subsequent studies in which phase 2 (generalization test) was omitted. This finding does not lend support to general theories of discrimination learning which emphasize error-elimination or inhibitory factors as being more important than excitatory factors.
10. See also H. Hanson [*J. Exp. Psychol.* **58**, 321 (1959)], for a study which tested these predictions along a visual-wavelength continuum; in that study, however, no direct determinations of inhibitory gradients were obtained.
11. H. S. Terrace, *Science* **154**, 1677 (1966).
12. In other words, "peak shift" was predicted for the 30° separation but was not obtained. However, T. M. Bloomfield [*J. Exp. Anal. Behav.* **10**, 361 (1967)] did observe more responding on a generalization test at —30° than at the positive stimulus of 0° in three of the five birds he trained with a negative stimulus of +45°. This was a greater separation of positive and negative stimuli than in our 30° separation, and thus peak shift should have been even less likely in Bloomfield's experiment. The reasons for this discrepancy are not clear.
13. See, for example, H. S. Hoffman, in *Punishment and Aversive Behavior*, B. A. Campbell and R. M. Church, Eds. (Appleton-Century-Crofts, New York, in press); and E. Hearst, in *Fundamental Issues in Associative Learning*, N. J. Mackintosh and W. K. Honig, Eds. Dalhousie Univ. Press, Halifax, in press).
14. Predictions based on algebraic summation of either absolute or relative gradients might be improved, and useful empirical knowledge might be gained, if the differential amount of time spent in phase 1 by the separate groups were somehow taken into account in further work. Because a discrimination criterion was used here, the groups of birds inevitably differed in the average amount of time spent in phase 1, particularly in the experiment involving the difficult separation of 30°. Data concerning the effect of amount of training on simple excitatory or inhibitory gradients have been recently reported [E. Hearst and M. B. Koresko, *J. Comp. Physiol. Psychol.* **66**, 133 (1968); G. W. Farthing and E. Hearst, *J. Exp. Anal. Behav.*, in press].

15. Supported by PHS grant MH 12120. I thank G. W. Farthing, M. Koresko, L. Shallenberger, and C. Ebbe for advice and assistance.

* Present address: Department of Psychology, University of California, Berkeley 94720.

8 August 1968

Mosaic Unit Ruler

The sequence of ratios that Moore has observed (*1*) in the dimensions of ancient Greek and Roman floor mosaics (known to mathematicians as the Fibonacci numbers) might be incorporated more economically in a ruler marked only (in units of 1.197 cm) at 0, 1, 2, 5, 13, 34, and 89. The other observed lengths, except for the extra one of 18 units (21.6 cm), would then be included as the distances between different pairs of marks on the ruler. An alternative would be a shorter ruler, with marks at 0, 1, 3, 8, 21, and 55, in which case the length of 18 units would be included (= 21 −3), while the length of 89 units (106.5 cm) would have to be obtained as the sum of 55 and 34, by placing the ruler twice.

ROBERT L. MILLS
Department of Physics,
Ohio State University, Columbus

Reference

1. R. E. M. Moore, *Science* **161**, 1358 (1968).

7 October 1968

Holoclemensia Instead of Clemensia

It has been brought to my attention that *Clemensia*, the name I proposed (*1*) for an Albian (Middle Cretaceous) didelphid marsupial, is preoccupied by *Clemensia* Packard of the Lepidoptera (*2*). I therefore replace *Clemensia* Slaughter with *Holoclemensia* Slaughter, 1968.

BOB H. SLAUGHTER
Shuler Museum of Paleontology,
Southern Methodist University,
Dallas, Texas 75222

References

1. B. H. Slaughter, *Science* **162**, 254 (1968).
2. *Proc. Entomol. Soc. Philadelphia* **3**, 100 (1864).

21 October 1968