

During the relatively brief period in which it was possible to maintain a steady level of moderately deep thiopental anesthesia, secondary discharges evoked by 0.5 per second ipsilateral sciatic nerve stimulation were unaltered in latency and configuration (Fig. 1B). At deeper levels of narcosis the first of a train of 0.5 per second stimuli evoked a maximal secondary discharge and relayed tract activity associated with the surface-positivity of the motor cortex response (Fig. 1G). Successive stimuli elicited secondary discharges of longer latency and complexity which were associated with marked increases in the latency of relayed tract responses (Fig. 1H). Under these conditions, corticospinal tract volleys, though considerably reduced in magnitude, were associated with a prominent very long-latency (150 msec) triphasic component of the cortical surface secondary discharge which evolved during repetitive (0.5 per second) stimulation (Fig. 1I). At this stage, secondary discharges were completely different in wave form from those recorded initially (Fig. 1G).

The finding that long-latency, generalized responses initiated by peripheral stimulation reflect activity in synaptic organizations linked to corticospinal neurons indicates that diffusely projecting *extrathalamic* pathways play an important role in the regulation of the corticospinal system. That a multiplicity of extrathalamic pathways may be involved in this regulation is evident from the variability of secondary discharges and associated relayed corticospinal tract discharges observed at different levels of barbiturate narcosis. In view of this, it is likely that such pathways may mediate effects on corticospinal neurons that have been reported to follow stimulation of diffuse peripheral fields under different experimental conditions (5).

Evidence is also presented here that diffusely projecting centripetal pathways activated by hippocampal efferents are capable of initiating corticospinal neuron discharges. This would appear to extend the range of action of archicortical efferent projection systems in the modulation of neocortical activity to a degree which has been previously unsuspected (6).

DOMINICK P. PURPURA
BERNARD COHEN*
GIOVANNI MARINI†

College of Physicians and Surgeons,
Columbia University, New York

References and Notes

1. A. Forbes and B. R. Morison, *J. Neurophysiol.* **2**, 112 (1939).
2. E. W. Dempsey, R. S. Morison, B. R. Morison, *Am. J. Physiol.* **131**, 713 (1941).
3. H. D. Patton and V. E. Amassian, *Handbook of Physiology, Neurophysiology* (American Physiological Soc., Washington, 1960), vol. 2, p. 837; K. Iwama and C. Yamamoto, *Electroencephalog. and Clin. Neurophysiol.* **13**, 2 (1961).
4. D. P. Purpura and E. M. Housepian, *Electroencephalog. and Clin. Neurophysiol.* **13**, 365 (1961).
5. V. B. Brooks, P. Rudomin, C. L. Slayman, *J. Neurophysiol.* **24**, 302 (1961); H. D. Patton, *Federation Proc.* **19**, 287 (1960).
6. This study was supported in part by the National Institute of Neurological Diseases and Blindness (B-1312 C3), the Parkinson's Disease Foundation, and the Sister Elizabeth Kenny Foundation.
- * Special research fellow, National Institute of Neurological Diseases and Blindness, U.S. Public Health Service.
- † Present address: Clinica Neurochirurgica dell'Università di Milano, Milan, Italy.

8 June 1961

Behavior Studies by Capacitance Sensing

Abstract. The movements of small burrowing animals submerged in sand are monitored through capacitance changes which detune radio-frequency oscillators. A new dimension of reptilian activity studies is possible by using this technique. Some early observations of several reptile species maintained in darkness in isothermal sand are given. Patterns of behavior during active phases, depth and rate of diving, and duration of quiescent periods are being revealed in detail for the first time.

The capacitance-sensing technique provides a potentially valuable tool for the ethologist and ecologist. Although the method is highly versatile, it apparently has not been used heretofore to study animal movements. One application of this technique is illustrated; extensions to other uses will suggest themselves readily.

Our initial studies have dealt with burrowing reptiles of the genera *Chionactis*, *Chilomeniscus*, *Anniella*, and *Lepotyphlops*. A wide variety of other lizards and snakes burrow with great facility in loose sand or soil. In desert regions, such burrowing animals often spend a large part of each day buried beneath the surface. It has been suspected that their subsurface stay is not always a simple quiescent period, but may involve movements related to temperature stratifications (1), food searching (2), or selection of moisture levels (2). The data relating to these suppositions are fragmentary and have resulted from observations of (i) humped-up surface soil or sand displaced by the shallowly buried animal (3), (ii) animals

submerged in glass-walled chambers and occasionally revealing themselves by pressing against the panes (1, 2), or (iii) the actual depths of buried animals uncovered by excavation (4). These methods give only a very incomplete picture of subsurface activity. A continuous monitoring method, allowing the investigator to detect the position of an animal constantly, is needed.

Capacitance sensing seemed most likely to fulfill this requirement. The method depends upon the production and detection of changes in capacitance of a regenerative radio-frequency oscillator. In the present application, the capacitance changes are brought about by the approach or contact of reptiles with a buried sensing element coupled with the oscillator condensers. Since the dielectric constant of sand is quite low (about 4), while that of animals is relatively high, the capacitance changes generated in this way are sufficient to make the method practicable.

Capacitance sensing has a number of advantages over other possible techniques: it is exceedingly sensitive (being able to detect large animals at distances over 15 inches); the sensing elements can be structured in any way desired; the geometry of the enclosure and environment is more or less immaterial; the experimental animals are undoubtedly insensitive to minute electrostatic fields oscillating at radio frequencies.

The enclosure illustrated in Fig. 1A was adopted after numerous trials. Its internal dimensions are $2\frac{1}{2} \times 18 \times 46$ inches. The $\frac{1}{4}$ -inch Plexiglas side panels are held in position by $\frac{1}{4} \times \frac{1}{4}$ -inch sand-tight grooves from which they are removable from above by sliding. External supporting structures are of wood.

The sensing and ground elements consist of linear grids of 24-gauge tinned copper wire strung back and forth with a horizontal spacing of $\frac{1}{4}$ inch. We have no reason to believe that the grids hamper free passage. Ten grids are spaced 4 inches apart, beginning 1 inch above the base. The grid-wire ends are fastened to binding posts on one side. These posts also serve as jacks to receive the oscillator lead-cables and grounds. The first, fourth, seventh, and tenth grids are used as sensors; the others are isolating grounds which reduce field coupling. The ground shield of each coaxial lead-cable is connected to both adjacent ground grids (except for the top and bottom shields).

For runs with an uncompacted fill, sand is poured into the chamber to the

desired level (usually 1 inch above the top grid). Sand stratified in this way can be compacted up to 10 percent by several sharp blows on the base of the chamber. At the end of a run, the sand is drained through outlets in the base. The final position of the animal can be ascertained at this time, for it usually resists the sand flow by clinging to the nearest grid.

Instruments Inc. Model B-04 oscillators (5) are employed. A regenerative radio-frequency oscillator of the Hartley type (Fig. 1B) is tuned into wide amplitude oscillation. The external sensing grid acts as a capacitance in series with the trimmer condensers. This series combination is effectively in shunt with the main fixed tuning condenser. When a burrowing animal touches or comes close to this grid, the capacitance of the tuned circuit is increased. A decrease in the amplitude of oscillation results, owing to interference in the coupling between the cathode and grid circuits of the 6SQ7 oscillator tube. As a result, current drawn by the diode plates of the 6SQ7 increases, with a consequent overriding of the bias of a thyatron. This triggers a relay to deliver an on-signal to the corresponding channel of an Esterline-Angus Event Recorder. False detuning of oscillators, caused by internally or externally generated power-line transients, can be eliminated by buffering the oscillators with line-voltage regulators.

The oscillators are tuned individually after the chamber has been filled with sand. The unit is then allowed to equilibrate for several hours and re-tuned before introducing the animal. Tuning may have to be readjusted during a run in which loose sand is employed, because sand compaction resulting from movements of the animal usually increases the dielectric constant of the fill. Tuning is carried out by readjusting the trimmer condensers of the oscillator tank circuit. We have sought to obtain position signals primarily on contact of experimental animals with the sensing grids. With this objective the most sensitive setting is unnecessary. Tuning is calibrated by consecutively contacting each sensing grid with two calibers of machine bolts mounted on Plexiglas rods. It is easy to tune the oscillators to fire the thyatron on contact of a given bolt with a binding post but not with the bolt of next size smaller. Even with this comparatively low sensitivity, an animal 9 or 10 inches long in contact with one

sensing grid can detune a second oscillator by approaching but not contacting its sensing grid. This commonly occurs when the experimental animal burrows nearly vertically. Such a record is shown in Fig. 1C. Oscillators can also be detuned by near approach of an animal in contact with a ground grid.

Thus far, movements have been monitored only in darkness in isothermal sand at a temperature (23° to 24°C) assumed to be within the limits of the animals' normal activity temperature ranges. Tests are planned with diurnal temperature gradients coincident with a daily light cycle. In this way, we hope to simulate subsurface thermal events and to give essentially

natural light cues. Behavior related to these factors should then become evident.

The tests in uncompacted isothermal sand show that the small colubrid snake, *Chionactis occipitalis*, and the limbless lizard, *Anniella pulchra*, are able to move up or down through the entire vertical depth of sand (38 inches) within as little as 7 minutes (Fig. 1C). Nearly every specimen of *A. pulchra* introduced into the chamber swam directly to the bottom. However, the patterns of movement are quite variable; they are interspersed with periods of quiescence, one of which lasted almost 45 hours (during which an oscillator was held continually detuned).

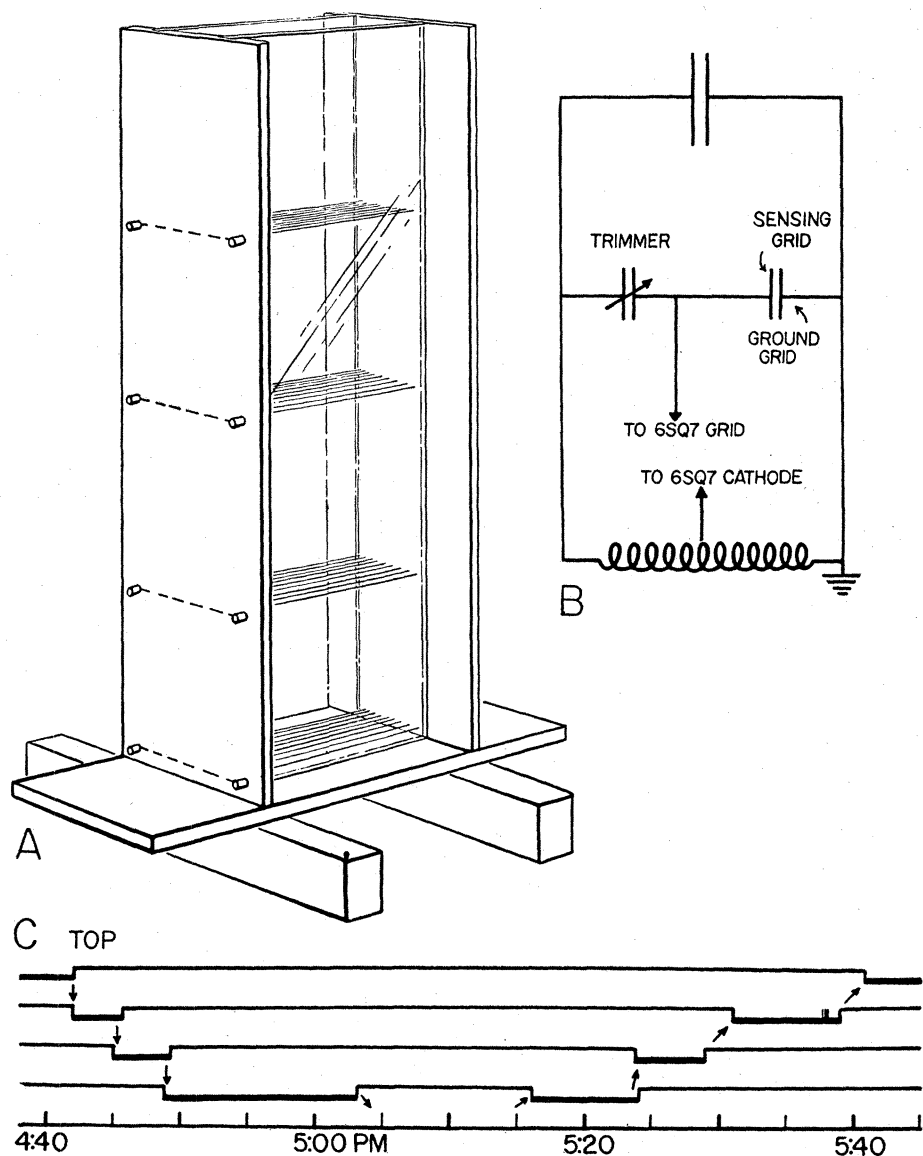


Fig. 1. A, Experimental enclosure (ground grids omitted). B, Simplified a-c circuitry of the Hartley oscillator. C, Esterline-Angus record of the movements of a 10-inch specimen of *Chionactis occipitalis* from near the surface of the sand to the bottom of the chamber (presumably below the bottom grid) and back in less than 1 hour. The on-signals of the recorder tracings are shown as heavy segments. Note that overlapping of on-signals occasioned by multiple detuning is most marked on the descent.

Recorded sorties at the surface are checked by inspection of the surface sand for tracks. Such tracks are smoothed so that subsequent sojourns at the surface can also be verified. It is interesting to note that smoothing surface sand does not disturb an animal resting within a fraction of an inch of the surface unless its body is actually touched.

Both *Chilomeniscus stramineus* and *Chionactis occipitalis* were often seen to rest near the surface with only an inch or so of the tail exposed. Similar behavior reported for *A. pulchra* (2) was not noted by us. Although its significance has not been established, a temperature-sensing function served by this behavior seems possible.

Future reports will deal with detailed records of movements and with the effects of thermal gradients (6).

J. LEE KAVANAU

KENNETH S. NORRIS

Department of Zoology, University of California, Los Angeles

References and Notes

1. L. M. Klauber, *Trans. San Diego Soc. Nat. Hist.* 9, 193 (1951).
2. C. M. Miller, *Ecol. Monographs* 14, (food searching) 274, (moisture levels) 284, (fossorial activity) 278, (temperature) 278 (1944).
3. W. Mosauer, *Copeia* 1, 15 (1933).
4. R. B. Cowles, *Ecology* 22, 134 (1941).
5. We are indebted to the Millard D. Shriver Co. of Rosemead, California, and Instruments Inc. of Tulsa, Oklahoma, for the loan of oscillators and other courtesies.
6. This work was supported by grant G-14533 from the National Science Foundation. We are indebted to Aaron Z. Klain for valuable technical consultations.

20 July 1961

Color Induction and Hue Discrimination

Abstract. A very close relationship has been found between hue discrimination thresholds and the differences in wavelength necessary to produce "full color" from two monochromatic light sources. This finding suggests a need for certain research in the area of color induction.

The experiments of E. H. Land (1, 2) demonstrating that many of the natural colors of the spectrum can be produced with only two monochromatic light sources, or one monochromatic source and white light, have stimulated much spirited discussion among persons interested in the study of color vision. The opinion held by most psychologists is that the effects produced by Land are not new and can be explained by mechanisms known to color theorists for many years. G. L. Walls (3) has pointed out that most of the colors which Land

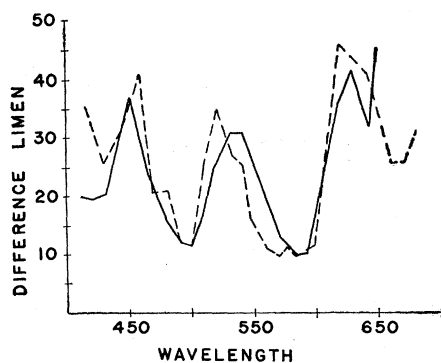


Fig. 1. Wavelength differences between projection primaries for a good effect (Land), dashed line, and hue discrimination thresholds ($\times 10$) (Hecht), solid line. The units of both axes are millimicrons.

produced can be explained by simultaneous color contrast or spatial induction—phenomena which have been familiar to psychologists for over 100 years. Viewed in this light, the Land effect loses much of its dramatic appeal as a possible source of a new theory of color vision.

There is one aspect of Land's work which does seem surprising to many psychologists: The wavelength separation between the two sources of monochromatic light which is necessary for the perception of colors other than the colors projected is surprisingly small. A difference in wavelength of about 45 m μ seems to be sufficient to produce "full color" regardless of the position on the visible spectrum from which the two light sources are selected.

I decided to see what relationship these spectral separations have to difference thresholds for wavelength discriminations. When two monochromatic lights of the same wavelength are presented to a human subject and the wavelength of one light is increased or decreased until the subject is able to discern a difference in hue between the lights, it is found that the amount of variation necessary is different for different points along the spectrum. These thresholds have been reproduced by Hecht (4) (using the data of Steindler, 1906) and show that the maximum difference limen is about 4 m μ and occurs in the red region of the visible spectrum.

Land (2) has given in his Fig. 3 a graph showing the color arrays obtainable with various combinations of wavelengths used in projecting two superimposed images on a screen. From this graph one can obtain the minimal separation of longer and shorter wavelengths required in different spectral

regions for a greater or lesser approach to "full color" in the projected picture.

The solid line in Fig. 1 shows the hue discrimination thresholds as reproduced by Hecht. These thresholds have been multiplied by 10. The dashed line represents the wavelength differences between projection primaries for a good effect as derived from Land's graph. These values are not multiplied by a constant.

One can see that there is a striking similarity between these two functions. The most obvious conclusion that can be drawn from this concomitant variation is that the production of "full color" from two monochromatic lights is dependent upon the existence of a sizable subjective difference in color between the two projection primaries. Thus, the three maxima of both functions correspond to regions of the spectrum in which a relatively large difference in wavelength is necessary to produce a subjective color difference. The interesting point to be made here is that it would appear from the graph that the wavelength separation necessary for "full-color" perception is some ten times as great as that necessary for a noticeable difference in hue.

Suppose that an annulus or ring of monochromatic light were projected upon a screen and that a second projector cast a spot of light of the same wavelength which filled the center of the annulus. If the wavelength of the surrounding annulus were varied, a point would be reached at which there would occur a noticeable change in the hue of the spot, despite the fact that the wavelength of the spot remained constant. On the basis of Walls's explanation of Land's findings and the relationship between the functions plotted in Fig. 1, one might expect that the change in wavelength of the annulus required to produce a change in the spot would be ten times that change required to cause a subjective difference in the hues of the spot and annulus (with each viewed through a mask which would prevent spatial induction).

LYLE W. BIVENS

Department of Psychology,
University of Colorado, Boulder

References

1. E. H. Land, *Proc. Natl. Acad. Sci. U.S.A.* 45, 115 (1959).
2. ———, *ibid.* 45, 636 (1959).
3. G. L. Walls, *Psychological Bull.* 57, 29 (1960).
4. S. Hecht, "Vision II. The nature of the photoreceptor process," in *Handbook of General and Experimental Psychology*, C. Murchison, Ed. (Clark Univ. Press, Worcester, Mass., 1934).

31 July 1961