XIX. COMMUNICATIONS BIOPHYSICS*

Prof. W. A. Rosenblith
Prof. M. A. B. Brazier†
Prof. M. Eden
Prof. M. H. Goldstein, Jr.
Prof. W. T. Peake
Prof. W. M. Siebert
Dr. A. E. Albert
Dr. J. S. Barlow‡
W. A. Clark**
Dr. B. G. Farley**
Dr. G. L. Gerstein
Dr. R. D. Hall
Dr. N. Y-S. Kiang
Dr. T. S. Sandel**

Dr. D. C. Teas
Dr. Eda Berger Vidale
Dr. T. Watanabe††
J. Allen
R. M. Brown
W. H. Calvin
R. R. Capranica
A. Crist
T. H. Crystal
J. W. Davis
Margaret Z. Freeman
J. L. Hall II
F. T. Hambrecht

J. G. Krishnayya
R. G. Mark
P. Mermelstein
C. E. Molnar‡‡
D. F. O'Brien
R. R. Pfeiffer
C. E. Robinson
E. N. Robinson
G. Svihula
Aurice V. Weiss
T. F. Weiss
J. R. Welch
M. L. Wiederhold
G. Wilde

S. K. Burns
R. J. Clayton
C. O. Compton
R. S. Fabry

R. G. Helmig
T. S. Huff
M. L. Jablow

K. C. Koerber
A. K. Ream
R. B. Stein
D. H. R. Vilkomerson

A. COMPONENTS OF THE RESPONSES EVOKED BY STIMULATION OF THE AUDITORY CORTEX OF ANAESTHETISED CATS

The auditory cortex of cats, anaesthetised with Dial, has been stimulated directly with electric pulses and indirectly by means of acoustic clicks. The responses evoked by shocks may be analyzed in five distinguishable components. A comparison of the responses to these two types of stimulation suggests that the 5-component analysis may also be valid for responses to clicks. Evidence is presented here to support the hypothesis that there occurs in the responses to clicks an early surface-negative component followed by a prolonged after-positivity.

1. Methods

The stimulating electrodes were made from two pieces of 10-mil tungsten wire of equal length, each tapered to an abrupt point and insulated within 100 microns of the tip. The separation between the tips of the wires was from one to one and a half

millimeters. The electrode pair was inserted perpendicularly to the cortex so that the points of the electrodes would be at an approximately equal depth below the surface. Doublets (i. e., pairs of pulses of opposite polarity)[1] were applied to the electrodes by means of a four-to-one step-up isolation transformer. Shock intensities were measured ahead of the isolation transformer and are given in decibels re 6 volts peak-to-peak. Clicks were produced by 100-μsec square pulses fed into a Permoflux PDR-10 headphone which was closely coupled into the external auditory meatus: their intensities are given in decibels re 1 volt into the headphone. Nineteen cats were used in this study. The animals were anaesthetised with Dial (0.75 cc/kg given intraperitoneally) and main-tained at rectal temperatures between 37° and 39°C. The auditory cortex was exposed and the stimulating electrodes placed in a region of maximal response to clicks on the side contralateral to the earphone. The electrodes were not advanced to a depth greater than 2 mm below the surface.

Monopolar recording electrodes were placed on the cortical surface at a distance of from 1 mm to 6 mm from the stimulating electrodes. The filters of the Offner ampli-fiers were set to pass the 2-1000 cps band. Signals from two or three different cortical
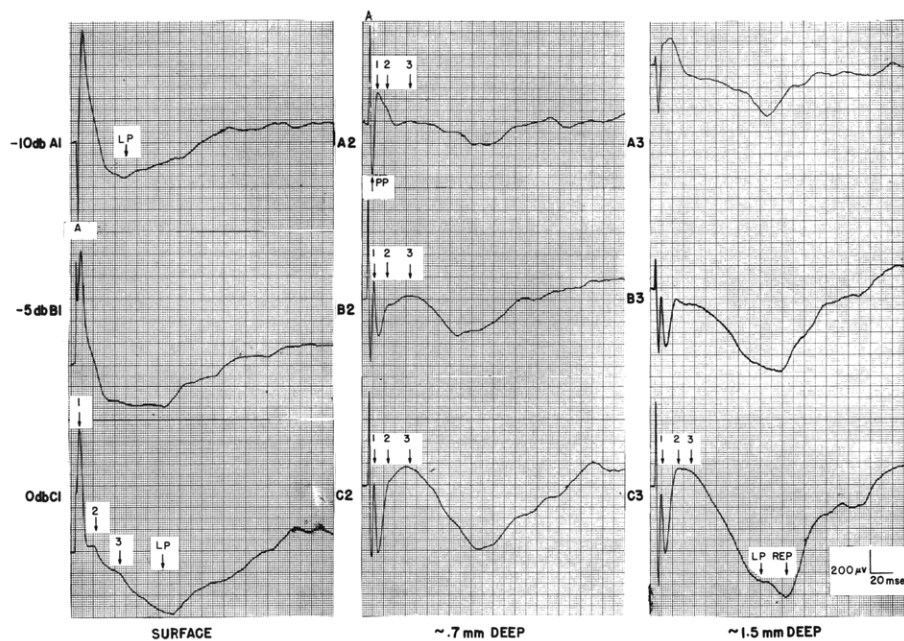
Fig. XIX-1. Effects of shock intensity and of depth of the stimulating electrodes on the shape of the response to single shocks. Rows indicate shock intensity; columns, electrode depth: 1. surface, 2. medium depth (approximately 0.7 mm), 3. deep (approximately 1.5 mm below surface). Arrows 1, 2, and 3 indicate components NC1, NC2 and NC3 (upward deflections); PP and LP (positive, downward deflec-tions); REP, repetitive wave. A represents shock artefact.

locations were recorded on magnetic tape and from 30 to 50 successive responses were averaged by means of the ARC-1 computer.[2]

2. Results

a. Components of the Evoked Responses

The responses evoked by shocks appear to be the sum of five different components. There are three surface-negative or negative-going "waves" which will be designated as the first (NC1), second (NC2), and third (NC3) components. The positive "waves" will be called primary positive (PP) and late positive (LP) (Fig. XIX-1). The contribution of each component to the composite waveform varies with shock intensity and
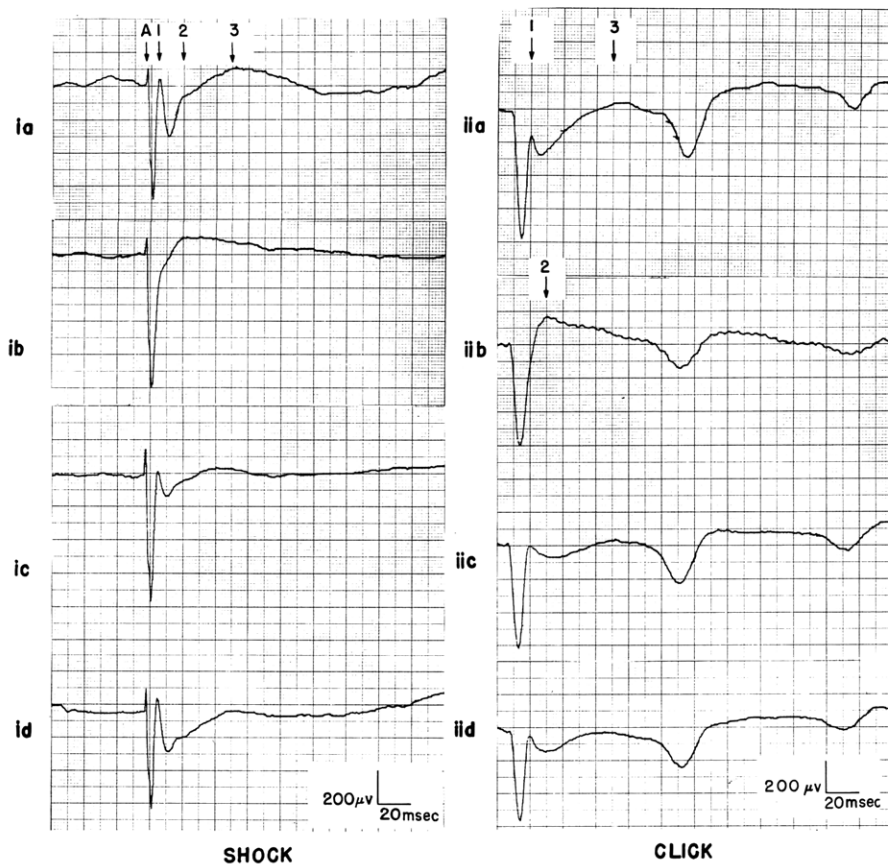
Fig. XIX-2. Local Novocain reduces the superficial components in the composite response to shocks (left, i), and a similar change in wave shape occurs in the response to clicks (right, ii). Records ia and iia show responses before application of Novocain; the subsequent records show responses at intervals 2-20 minutes after application. Both columns of these records are from the same cortical location: a series of 30 clicks alternates with a series of 30 shocks (shocks, 0 db; click, -60 db). 1, 2 and 3 indicate negative components as in Fig. XIX-1. Shock artefact is indicated by A.

depth of insertion of the stimulating electrodes. When the electrode tips are not far below the cortical surface (less than ~0.3 mm) the response consists mainly of the components NC1, NC2, and LP (Fig. XIX-1, column 1). These components will, therefore, be referred to as the "superficial" components. The LP wave invariably accompanies the NC1 component and is never present if NC1 is absent. It will be assumed that the LP wave represents hyperpolarization in the elements that generate NC1.

As the electrodes are further advanced into the cortex the form of the response changes owing to the addition of the "deep" components, namely, the PP wave and the third negative component (NC3) (Fig. XIX-1, columns 2 and 3). NC3 is very prominent in the records and tends, for the interval from 20 msec to 70 msec after stimulus delivery, to obscure LP. However, for strong shocks, LP outlasts NC3 and reappears at from 80 msec to 100 msec after stimulus delivery (Fig. XIX-1, rows B and C).

With the electrodes deep in the cortex and with very strong shocks (Fig. XIX-1, column 3) a repetitive wave (REP) appears in the record. This component is not believed to be part of the primary response and will not be considered further — all five components of the primary response to shocks remain after the cortex has been undercut with a length of wire. Similar results have been reported by Goldring et al.[3]

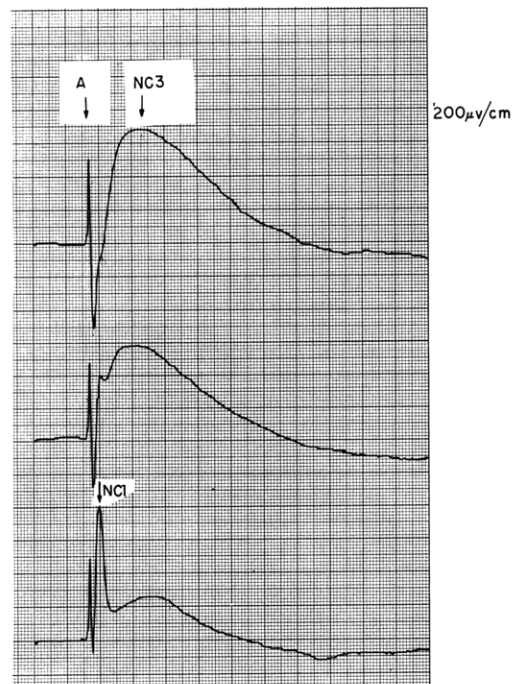Strong shocks delivered to the deeper layers of the cortex yield a composite response

Fig. XIX-3. Effect of local Dial on the response to shocks. Top record: two minutes after application of Dial. Subsequent records show recovery. Note that NC1 regains amplitude as NC3 declines. Shock strength, −5 db. Shock artefact is indicated by A.

the initial part of which has a characteristic W-shape. The second positive-going deflection in the W is presumed to be, not a separate component, but the result of the superposition of PP, NC1, and the start of LP. The composite response resembles the "notched" response to clicks.[4] This similarity suggests that the negative-going pinnacle in the notched response (indicated by the number 1 in Fig. XIX-2 iia, and Fig. XIX-4) corresponds to the first negative component NC1 of the response to shocks and that the subsequent positive-going deflection is due largely to the presence of an LP wave. Tentative identification of NC2 and NC3 in the responses to clicks has also been made and these are indicated as 2 and 3 in Fig. XIX-2.

The evidence in the following sections appears to substantiate the proposed identification of common components in responses to shocks and clicks.

b. Local Application of Novocain and Dial

Local application of one drop of 2 per cent Novocain eliminates, or greatly reduces, the contribution of the superficial components to the composite shock response and diminishes the corresponding components in the evoked response to clicks. In the case illustrated (Fig. XIX-2) it is especially NC1 and LP that are affected, while the small NC2 is undiminished. In the click response NC2 appears in record iib but during the recovery process it is again obscured by the LP which reappears together with NC1.

The effect of local application of Dial on the responses to shocks resembles the effect of Novocain except that NC3 is greatly increased in the presence of Dial (Fig. XIX-3). Intraperitoneal Dial administered to a cat already lightly anaesthetised, likewise reduces the amplitude of NC1. These observations suggest a mechanism for the disappearance of the "notch" in the click response under deep anaesthesia.

c. Responses to Paired Stimuli

NC1 is always diminished in the response to the second stimulus, provided that the two stimuli are separated by not more than 200 msec. (For any pair of stimuli the behavior of NC2 and NC3 cannot be summarized so succinctly). The extent to which NC1 is reduced in the response to a click (C) that has been preceded by a shock (S) depends both on the intensity of the shock (Fig. XIX-4) and the shock-click interval. The reduction of NC1 in the click response is readily produced when the click is preceded by a shock that elicits only the superficial components of the shock response. These results suggest that the elements responsible for NC1 undergo a prolonged phase of reduced responsiveness following their activation. The cellular counterpart of this reduction of responsiveness is probably a hyperpolarization of the cell membrane. LP, which always follows NC1, may well be an indicator of this hyperpolarization in the superficial elements that give rise to NC1.

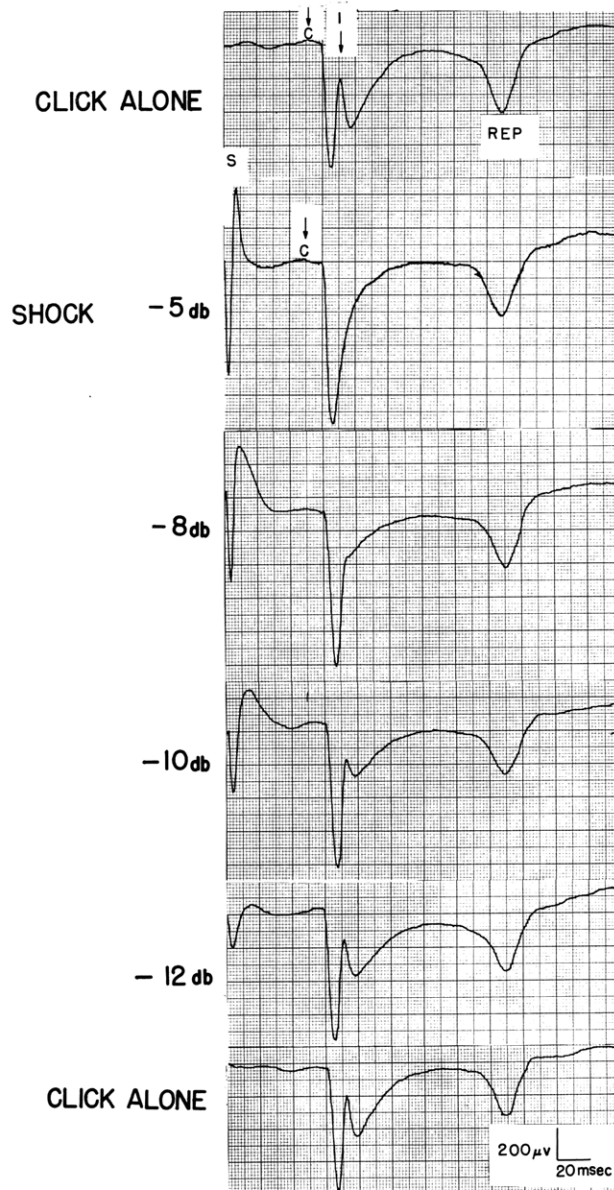Fig. **XIX**-4. Effect of shocks of different strengths on a subsequent response to clicks. Shock intensities indicated at the left; click, −60 db; S and C indicate instants of stimulus delivery; REP is the repetitive component of the click response.

(XIX. COMMUNICATIONS BIOPHYSICS)

3. Discussion

Though certain differences in experimental techniques may have prevented Goldring et al.,[3] from observing a W-shaped response, their conclusions regarding individual components of responses to shocks are in agreement with those given above. Chang[5] whose cats were in all likelihood more deeply anaesthetised than our preparations described only three response components (neither NC2 nor LP were observed). Although neither Goldring or Chang attempted to relate shock responses to click responses, Bishop and Clare[6] have demonstrated that responses to shocks delivered deep in the visual cortex strongly resemble response to flashes.

The evidence presented here makes it appear unlikely that the superficial cortical layers are excited only by slow conduction along dendrites or by cortical interneurones. On the contrary, the evidence indicates either that branches of radiation fibres extend to the superficial layers or, as suggested by von Euler and Ricci[7] that there is an independent radiation supply to these layers. The whole problem of the boundary between the "deep" and "superficial" layers deserves further study, especially in relation to the locus of "potential inversion" for the early surface-positive and early surface-negative waves.

Neuroanatomical and microelectrode studies are needed to supplement the crude analysis into components given here and elsewhere. Finally, unanaesthetised preparations need to be studied in conditions in which dc potential shifts can be recorded together with the potential changes reported here.

Clare Monck

(This research was conducted from March to August 1961, when Miss Monck was a member of the Communications Biophysics Group.)

References

1. J. C. Lilly, J. R. Hughes, E. C. Alvord, Jr., and T. W. Galkin, Brief non-injurious electric waveform for stimulation of the brain, Science, 121, 468-469 (1955).

2. W. A. Clark, R. M. Brown, M. H. Goldstein, Jr., C. E. Molnar, D. F. O'Brien, and H. E. Zieman, The average response computer (ARC): A digital device for computing averages and amplitude and time histograms of electrophysiological response, Trans. IRE, Vol. BME-8, pp. 46-51, 1961.

3. S. Goldring, J. O'Leary, T. G. Holmes, and M. T. Jerva, Direct response of isolated cerebral cortex of cat, J. Neurophysiol. 24, 633-650 (1961).

4. N. Y-S. Kiang and M. H. Goldstein, Jr., Evoked cortical responses and anesthesia, Quarterly Progress Report, Research Laboratory of Electronics, M.I.T., July 15, 1957, pp. 142-144.

5. H-T. Chang, Dendritic potential of cortical neurons as produced by direct electrical stimulation of the cerebral cortex, J. Neurophysiol. 14, 1-21 (1951).

6. G. H. Bishop and M. H. Clare, Responses of cortex to direct electrical stimulation applied at different depths, J. Neurophysiol. 16, 1-19 (1953).

7. C. von Euler and G. F. Ricci, Cortical evoked responses in auditory area and significance of apical dendrites, J. Neurophysiol. 21, 231-246 (1958).

B. SOME RESPONSE CHARACTERISTICS OF SINGLE UNITS IN THE COCHLEAR NUCLEUS TO TONE-BURST STIMULATION

In continuing studies of single units in the cat's cochlear nucleus attempts are being made to quantitatively categorize units on the basis of their response characteristics to acoustic stimuli.[1] In these studies, wide assortments of response patterns have been observed. Despite this broad spectrum of patterns, some common features have been found. In particular, for a majority of the units studied, the responses to tone-burst stimulation exhibit preferred times of firing relative to the onset of the stimulus time (PST) histograms.[2]

Figure XIX-5 shows PST histograms for eight different units in response to tone bursts. This display is a histogram of times of occurrence of spike responses referred to the time of stimulus onset. In each of these units there is a sharp increase in activity at the onset of the tone burst, and an abrupt decrease at the termination of the stimulus. In every case the unit fires at particular times during the tone burst which are spaced somewhat regularly. The peaks of the histograms of units 11-6, 19-5, 21-4, and 23-6 are quite distinct throughout the duration of the burst. The widths of the peaks in the histogram become progressively larger during stimulation. As a result of this increase in width, the later peaks of the histograms of units 9-5, 9-7, 13-9, and 22-3 become less distinct. Of approximately 150 cochlear nucleus units studied, approximately three-quarters show preferred times of firing at the onset of stimulation.

In this report we shall be concerned with the dependence of this behavior on stimulus parameters. In particular, we shall discuss systematic changes in the time interval between peaks in the PST histogram and in the latency of the mode of the initial peak of the histogram.

Figure XIX-6 shows average patterns of activity for one unit for different intensities of stimulation. Column 1 consists of histograms of intervals between spikes,[2] and column 2 of PST histograms for the same data samples. It can be observed from the PST histograms that the interpeak intervals and the latency of the mode of the initial peak decrease monotonically with increases in the stimulus intensity. It also can be seen that the mode of the interval histograms (left-hand column) closely correspond to the intervals between peaks of the PST histograms. The mode of the interval histogram will be used here as a convenient measure of the average interpeak time of the PST histogram. The absence of additional peaks in the interval histogram indicates that for each presentation of the stimulus this unit responds with a spike at every "preferred time."
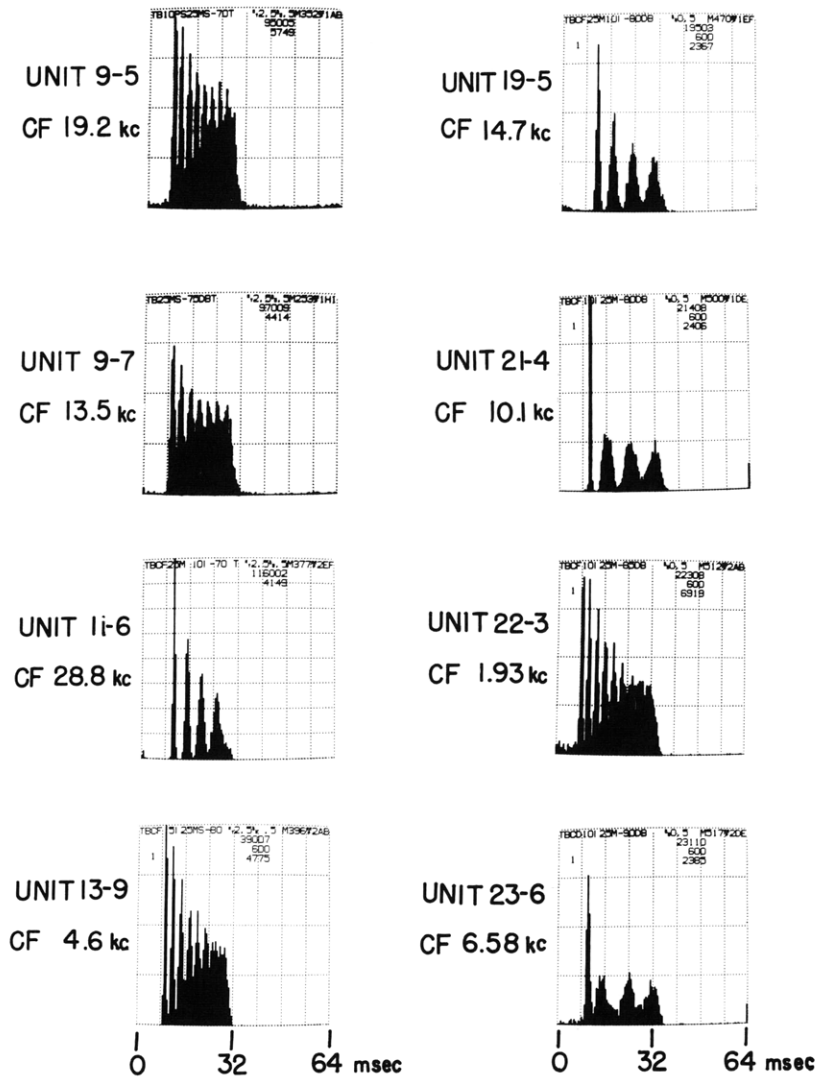
Fig. XIX-5.   Poststimulus time histograms for eight units in the cochlear nucleus. Latency is plotted on the abscissa; the ordinate shows the number of responses occurring in each 0.5-msec time interval after delivery of the stimulus. Each ordinate division corresponds to 64 events. Each histogram was obtained from 1-minute data samples. Stimulus: 25-msec tone burst; with 2.5-msec rise and fall time. The frequency of the tone burst was at the "characteristic frequency" (CF) of the unit (CF is defined as that frequency for which the threshold is lowest). In the data presented the frequency of the tone bursts is always at the "characteristic frequency" of the unit. However, these preferred firing times are also present for frequencies other than the CF. Stimulus repetition rate, 10/sec. Intensity of the stimuli in db above threshold for visual detection of synchronized responses on an oscilloscope (UVDL--unit visual detection level): 13, 10, 5, 6, 19, 20, 23, and 11 for units 9-5, 9-7, 11-6, 13-9, 19-5, 21-4, 22-3 and 23-6, respectively.
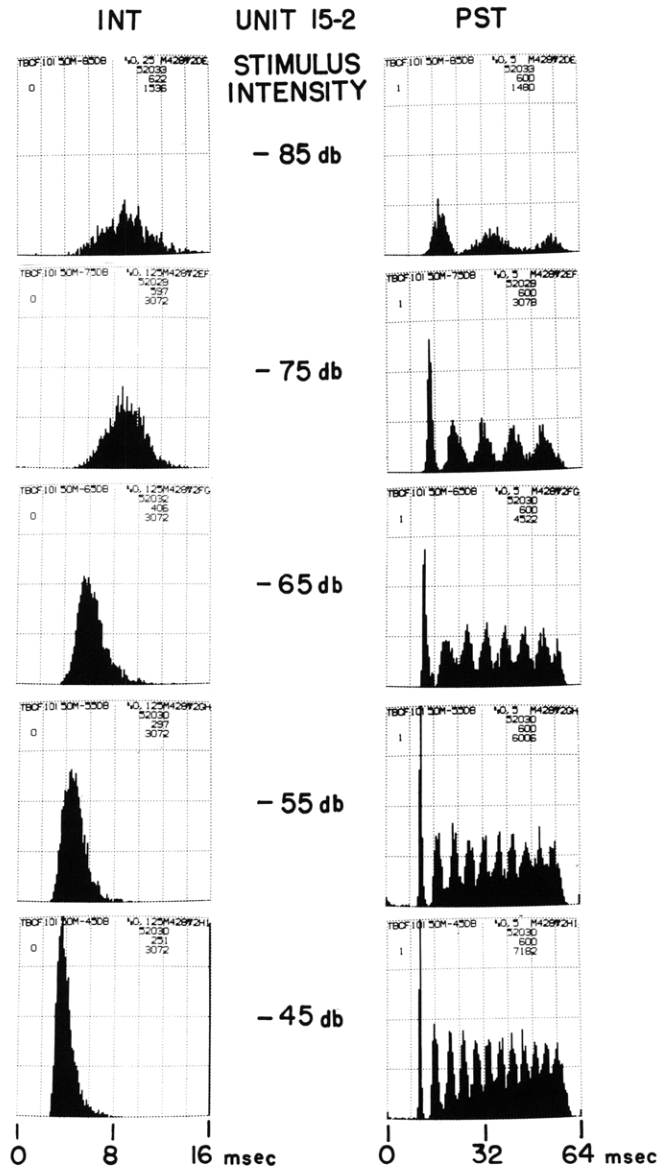
Fig. XIX-6. PST and interval histograms for 5 stimulus intensities. UVDL, −100 db re 2 volts peak-to-peak into the earphone. Each PST histogram was obtained from 1-minute data samples. The interval histograms were obtained from 3072 intervals, except the one for −85 db which is from 1536 intervals. The group of long intervals corresponding to the time from the last spike during stimulation to the first spike in response to the next stimulus (~50 msec) is not shown because of the time scale of the histograms. Stimuli: 50-msec tone bursts; 2.5-msec rise and fall time. The frequency of the tone burst was the CF of the unit (14.2 kc). Stimulus repetition rate, 10/sec. Each vertical division is for 64 events.
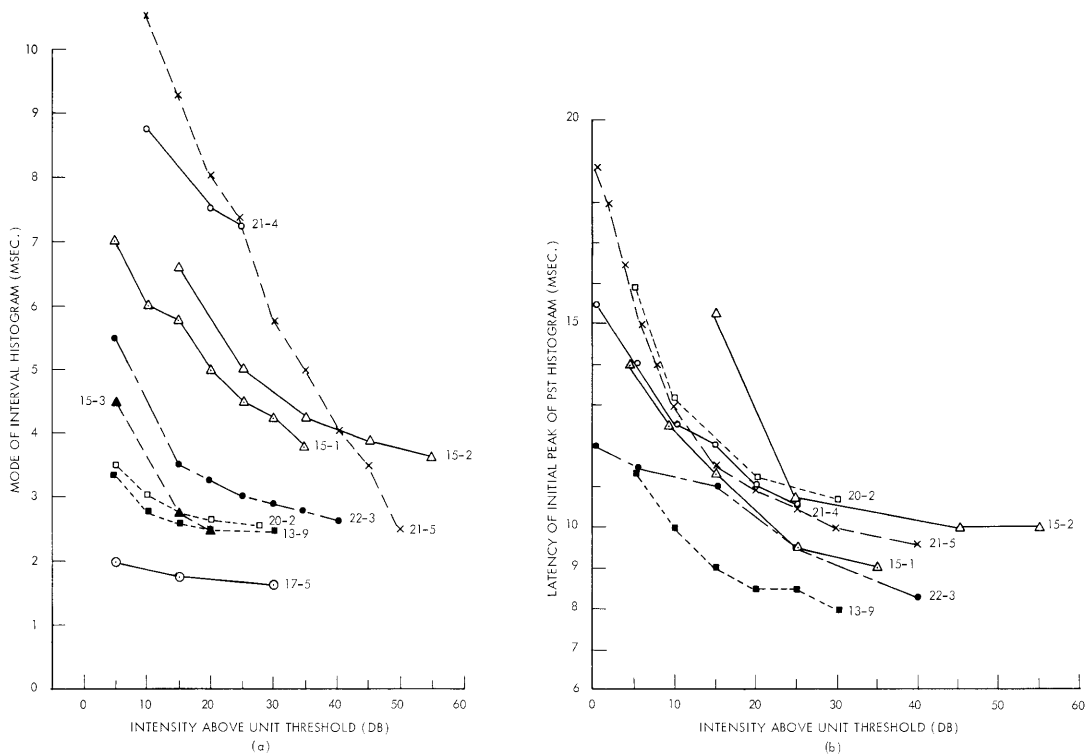
Fig. XIX-7. (a) Mode of interval histograms vs intensity of stimulus. Reference
intensity (0 db) for each unit corresponds to UVDL for that unit.
Stimulus: a 25-msec tone burst; a 2.5-msec rise and fall time.
The frequency of the tone burst was the CF of the unit. Stimulus
repetition rate, 10/sec. The points were obtained from 1-minute
data samples. The characteristic frequencies in kc: 4.6, 13.7,
14.2, 2.2, 21.1, 4.1, 10.1, 6.9, and 1.9 for units 13-9, 15-1, 15-2,
15-3, 17-5, 20-2, 21-4, 21-5, and 22-3, respectively. These char-
acteristic frequencies are estimated to be accurate within ±0.2 kc.
(b) Latency of the mode of the initial peak of the PST histograms vs
intensity of the stimulus for the same data samples as in (a). In
some cases, peaks in the histograms were distinct enough to allow a
measurement of latency at UVDL.

309
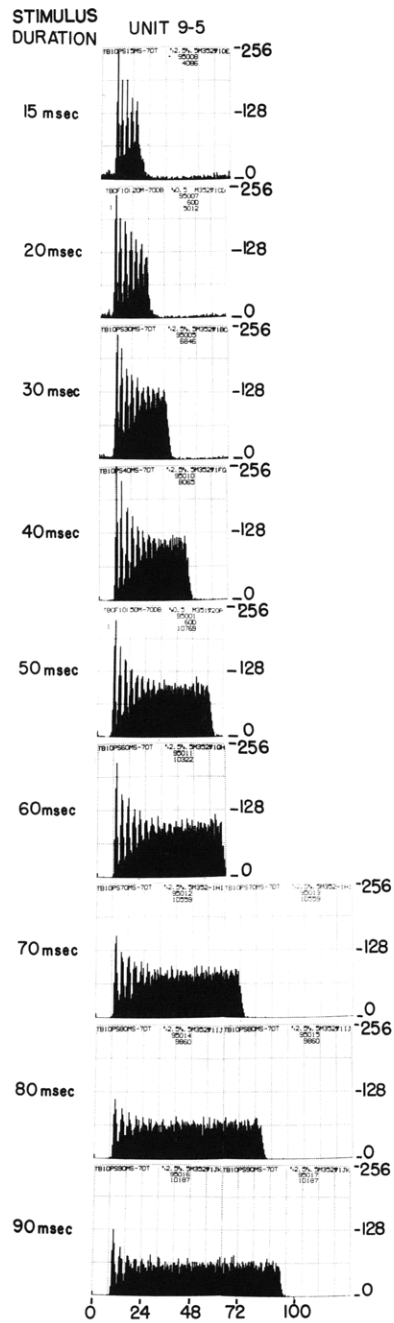
Fig. XIX-8.   Poststimulus time histograms for a duration series. The duration
of the stimulus is indicated for each histogram. Each PST histo-
gram was obtained from 1-minute data samples. The tone bursts
were at the characteristic frequency of the unit (13.2 kc) with a
2.5-msec rise and fall time and presented at a 10/sec repetition
rate. The intensity of the stimulus was 13 db above the UVDL.
The full ordinate scale in each case represents 256 events. The
abscissa scale has a 0.5-msec quantization interval.

Fig. XIX-9. (a) Mode of interval histograms vs duration of the stimulus. The points were obtained from 1-minute data samples. In each case, the stimulus was at the characteristic frequency of the unit. The tone bursts had a 2.5-msec rise and fall time and were presented at a 10/sec repetition rate. Intensity in db of the stimuli above UVDL: 13, 3, 6, 30, 12, 15, 10, and 11 and the characteristic frequencies in kc were 13.2, 15.0, 4.6, 13.5, 8.2, 6.4, 10.1, and 2.7 for units 9-5, 13-3, 13-9, 13-12, 14-6, 14-9, 21-4, and 23-6, respectively (CF's ±0.2 kc).
(b) Latency of the mode of the initial peak of the PST histograms vs duration of the stimulus for the same data as in (a).

311

STIMULUS   UNIT II-6
REPETITION
RATE

5/sec

10/sec

15/sec

20/sec

25/sec

30/sec

35/sec

```
I   I      I
0   32    64 msec
```
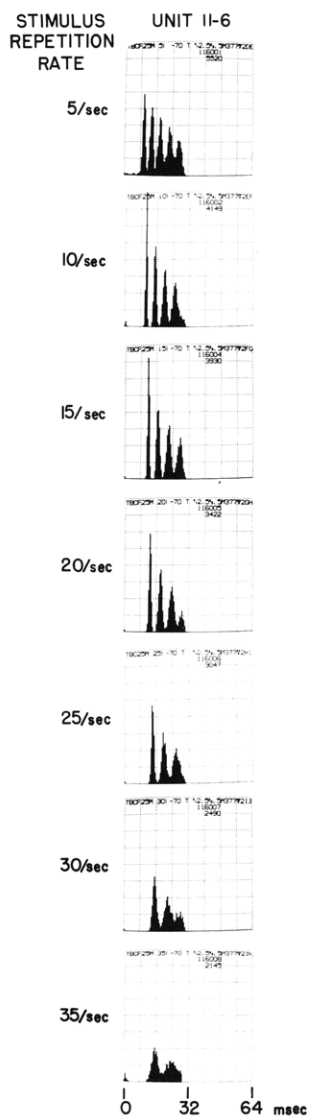
Fig. XIX-10. Poststimulus time histograms for a rate series run. Each PST histogram was obtained from responses to 600 stimuli. The tone bursts were 25 msec in duration, at the characteristic frequency of the unit (28.8 kc), with a 2.5-msec rise and fall time. The intensity of the stimulus was 5 db above UVDL. The full ordinate scale in each histogram represents 512 events. The abscissa scale has a 0.5-msec quantization interval.
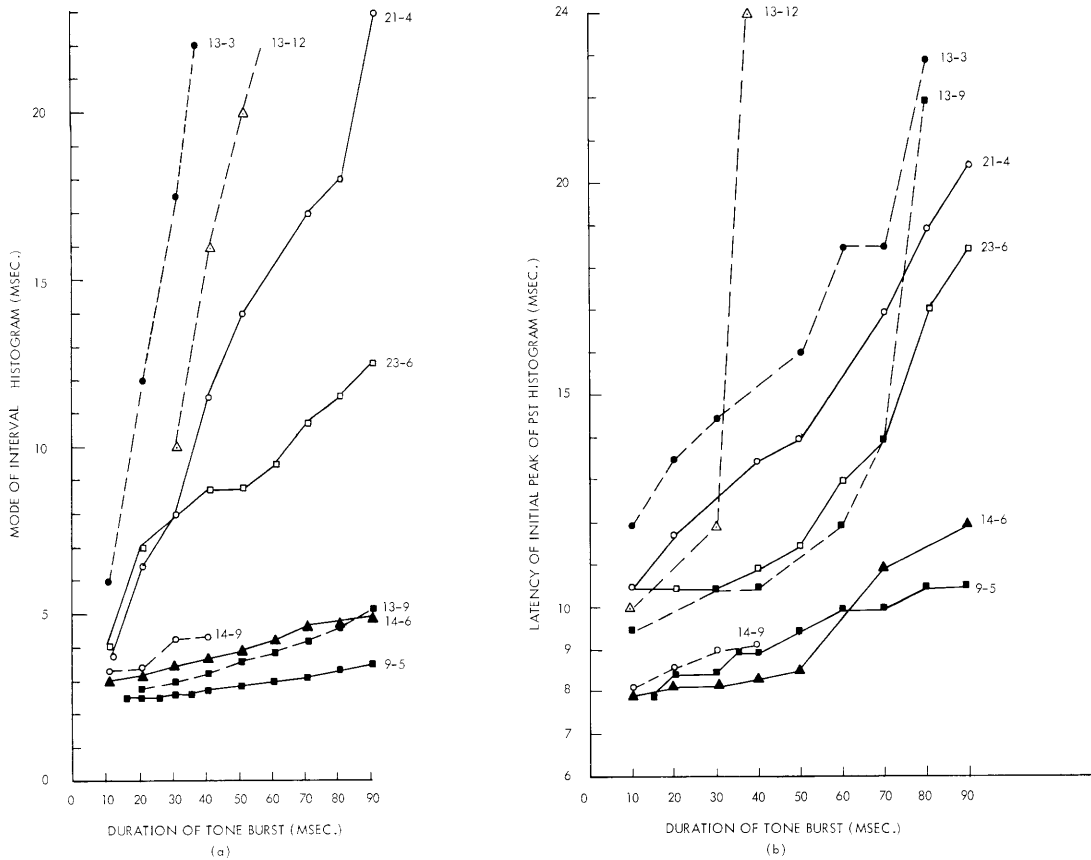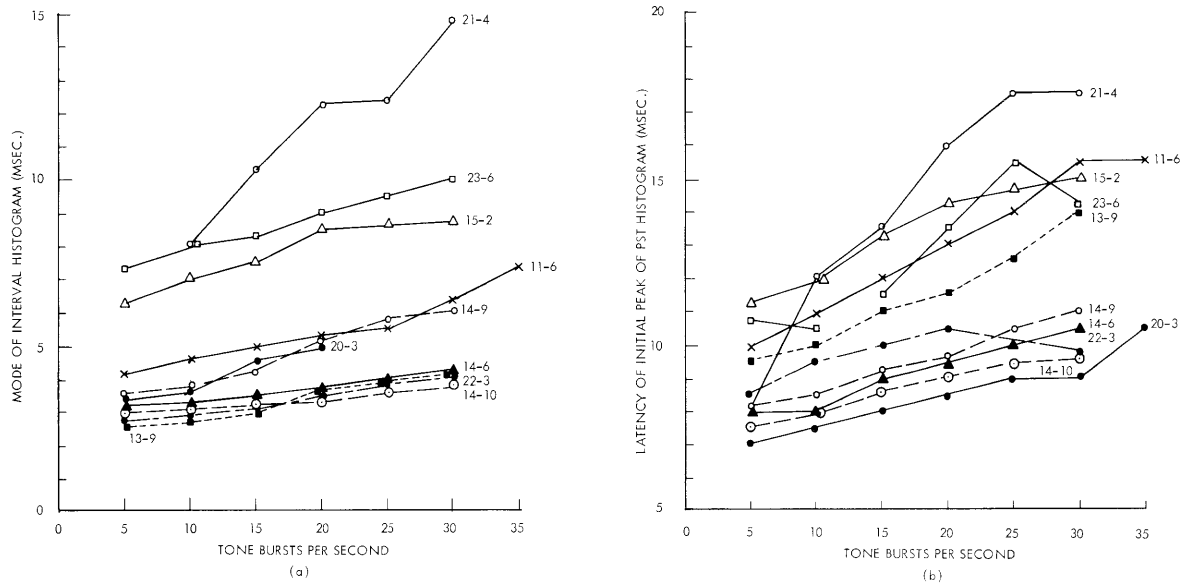
Fig. XIX-11. (a) Mode of interval histograms vs stimulus repetition rate. The points were obtained from responses to 600 stimuli. In each case, the stimulus was a 25-msec tone burst at the characteristic frequency of the unit. The tone bursts had a 2.5-msec rise and fall time. Intensities in db of the stimuli above UVDL: 5, 6, 12, 15, 15, 25, 28, 10, 23, and 11, and the characteristic frequencies in kc were 28.8, 4.6, 8.2, 6.4, 14.2, 5.4, 1.6, 10.1, 1.9, and 2.7 for units 11-6, 13-9, 14-6, 14-9, 14-10, 15-2, 20-3, 21-4, 22-3, and 23-6, respectively.
(b) Latency of the mode of the initial peak of the PST histogram vs stimulus repetition rate for the same data samples as in (a).

Figure XIX-7 shows data obtained from intensity series for 9 units. Each point was obtained from histograms similar to those shown in Fig. XIX-6. In Fig. XIX-7a the mode of the interval histogram is plotted as a function of stimulus intensity. Figure XIX-7b is a plot of the latency of the mode of the initial peak of the PST histogram against stimulus intensity for the same set of units. In every case, the modes decrease monotonically with increases in intensity. It is also apparent that the total change of the modes varies considerably from unit to unit.

Figure XIX-8 shows the PST histograms for one unit for stimulation by tone bursts of different durations. For this duration series, the interpeak interval and the latency of the mode of the initial peak of the PST histogram increases monotonically with increases in the stimulus duration.

Figure XIX-9 shows duration series data for a number of units. Figure XIX-9a is a plot of the mode of the interval histograms against the duration of the stimulus. Figure XIX-9b is a plot of the latency of the mode of the initial peak of the PST histogram against the duration of the stimulus for the same set of units. It is apparent in each case that both the mode and the latency increase monotonically with the duration of the stimulus. Here, too, large variations in the magnitude of these changes occur from one unit to another.

Figure XIX-10 shows an example of variations in the PST histograms with changes in the rate of the tone-burst stimulation. These histograms clearly illustrate that both the interpeak interval and the latency increase monotonically with increases in stimulus repetition rate.

Data from rate series for a number of units are shown in Fig. XIX-11. Monotonic changes of the interpeak interval for changes in the stimulus repetition rate occur in every case. All of the units show a monotonic increase in latency with stimulus rate, except for units 22-3 and 23-6 at the highest rates.

Summarizing, the PST histograms of single-unit responses to tone-burst stimulation exhibit distinct peaks. This illustrates preferred times of unit firing at the onset of stimulation. The interpeak intervals and the latency of the mode of the initial peak of the PST histogram change systematically with changes in stimulus parameters for all of these units. The interpeak interval and the latency decrease monotonically with increases in stimulus intensity, and decrease monotonically with increases in stimulus duration or stimulus repetition rate. Thus far, neither the interpeak interval, nor the latency of the initial peak of the PST histograms, show any obvious correlation with other properties of the units, e. g., spontaneous activity, characteristic frequency, unit threshold, individual animal or electrode position.

R. R. Pfeiffer

References

1. N. Y-S. Kiang, A category of cells in the cat's cochlear nucleus defined by electrophysiological experiments, Quarterly Progress Report No. 61, Research Laboratory of Electronics, M. I. T., April 15, 1961, pp. 179-183.

2. G. L. Gerstein, Analysis of firing patterns in single neurons, Science 131, 1811-1812 (1960).

C. CORTICAL CORRELATES OF BEHAVIORAL STATES IN THE RAT

With the increasing experimental interest in the neuroelectric phenomena underlying learning, attention, and other complex behavioral processes, the rat will undoubtedly come into its own as a preferred subject in electrophysiological studies of the behaving organism. Thus far, however, relatively little is known about the electric activity of the central nervous system of the unanesthetized rat. A number of investigations[1-7] have been concerned with on-going activity (EEG or ECG) in this system, but their concern has been primarily with changes in the activity effected by the administration of drugs or by special operations, for example, adrenalectomy. Moreover, in most of these studies some sort of restraint was imposed upon the animals in order to make possible the electrical recording. There are, then, few systematic data on the cortical activity from the unrestrained rat, particularly with respect to the ways in which this activity may vary as a function of behavioral state. The data reported here represent our first attempt to characterize the electrocorticogram (ECG) of the rat.[8]

Extradural electrodes were implanted in three animals (stainless-steel wire 0. 01 in. in diameter). Symmetrical pairs of electrodes were placed over right and left hemispheres: the anterior electrode of each pair over the somatosensory cortex, the posterior one over the visual area. Recordings were made of the potential differences between these sites. Neck-muscle potentials were recorded through a third pair of electrodes: one of these was cemented to the posterior aspect of the occipital bone, and a reference electrode was placed at the extreme anterior part of the cranial cavity, at the tips of the olfactory bulbs. The latter placement was chosen with the possibility of using it as a common reference for all of the other electrodes. The three pairs of electrodes were brought to small hearing-aid sockets that were fastened to the skull by dental cement and stainless-steel screws. Fine leads, protected by a steel spring sleeve, provided connections to the amplifiers and permitted the animals to have almost complete freedom of movement.

Cortical and neck-muscle potentials were monitored on oscilloscopes; throughout each experimental session the muscle potentials were also led to an rms voltmeter. Gross changes in state were clearly visible on both monitors. The potentials were recorded on magnetic tape and subsequently played back for computation of correlograms

315

and to obtain conventional ink records.

The experimental environment consisted of a small box enclosed in a larger chamber that was acoustically insulated and electrically shielded. The animals were observed through a small window.

Twelve to 18 hours before an experimental session the animals were placed in a motor-driven wheel. Throughout this exercise period they were also deprived of food. Food and water, however, were available to the animals during the entire recording period. These procedures were employed in order to obtain an ordered sequence of behavioral states and to insure that sleep would be encountered within a session of reasonable length.

In one series of experiments the chamber was illuminated and a wideband acoustic noise was present to mask any extraneous sounds. In a second series both light and noise were removed. The data obtained from unanesthetized animals were supplemented by recordings obtained while the animals were under barbiturate anesthesia. Anesthetization was accomplished by a single intraperitoneal injection of 0. 1 cc of Nembutal per 100 grams of body weight. Records of the electric activity were taken 30 minutes after body relaxation became evident.

The potentials recorded from each hemisphere were autocorrelated and the recordings from the two hemispheres were crosscorrelated. The computations were performed on an analog device designed by Barlow and Brown.[9] The correlograms were computed from 3-minute samples; maximum delays of 1 sec were usually employed.

It became clear at the outset of the experiments that it would be extremely difficult to obtain homogeneous samples of the cortical activity when the animals were in a highly aroused and active state. Under most circumstances the variability in the behavior and the corresponding changes in the cortical activity were prohibitive in this respect. One possibility did present itself: When given food after being placed in the chamber, an animal would sit and eat consistently for periods of 5 minutes, or more. The cortical activity recorded while this highly motivated behavior was in progress has been taken to be reasonably representative of the ECG in the aroused animal.

When the animals were eating, the cortical activity was of moderate amplitude and exhibited appreciable high-frequency content. Neck-muscle potentials were exceedingly large and were also of high frequencies. Typical records of the cortical and neck activity obtained while the animals were eating can be seen at the top of Fig. XIX-12. It should be noted that the muscle potentials, particularly, have suffered appreciable reduction as a result of the frequency characteristics of the recording system and ink writer. The correlograms exhibit rhythmic activity, but the intervals between peaks in the correlograms are somewhat variable, even within single samples. This activity is almost certainly related to the chewing movements. It is of interest, however, that these oscillations could not be detected in the ink records and were discovered only in
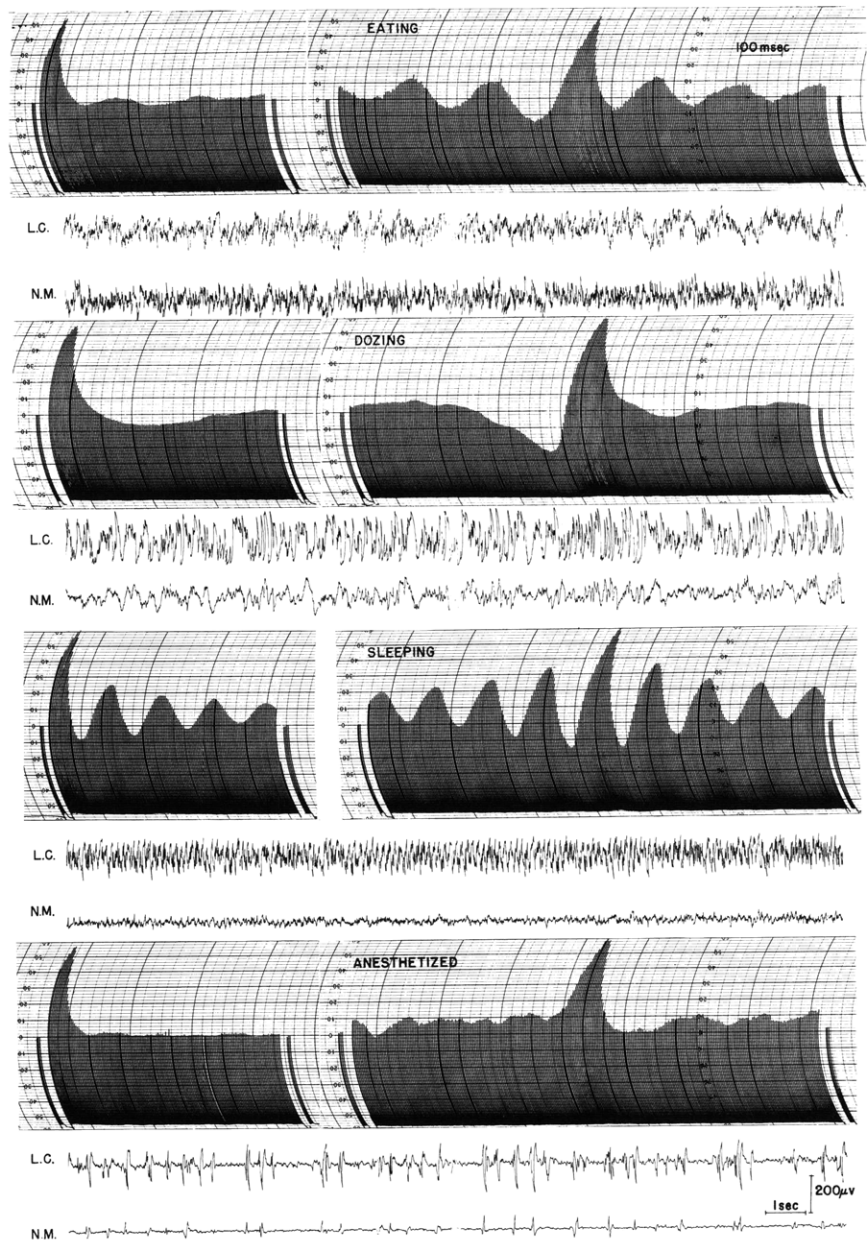
Fig. XIX-12. Changes in ECG as a function of state for Subject 3. Autocorrelograms in the left column are for left hemisphere; crosscorrelograms in the right column are for right and left hemispheres. $\Delta\tau$ is 4 sec, and maximum delay is 600 msec for both. LC represents ECG from left cortex; N. M., neck-muscle potentials for the corresponding period. Note that the vertical scales are arbitrary and different for the various correlograms. Zero delay in all correlograms occurs at the largest peak.

the correlograms, samples of which are also shown in Fig. XIX-12.

After an hour or more of eating, the animals spent some time in grooming and exploratory behavior. There were no obvious changes in cortical activity during this period except that the muscle potentials no longer reflected the rhythmic movements of chewing, but rather reflected a variety of other activities.

The next clearly differentiable state occurred when the animals lay down and remained virtually motionless for some time. The cortical potentials became much larger and "slower" than those recorded when the animals were eating. The neck potentials were also slower, but their rms value was approximately 90 μv as compared with 40 μv obtained in the active animal. Examples of these potentials can also be seen in Fig. XIX-12, in which representative ink tracings and the corresponding correlograms are presented. The correlograms display no prominent rhythmic activity.

It has been extremely difficult to apply a conventional label to this state characterized by the large slow cortical potentials. The activity of both cortex and neck muscle seems to indicate that a single state is under observation, but we are not at all sure that this is the case. Within these periods there are times when the animals, with eyes closed, appear to be sleeping; at other times they appear to be awake, that is, their eyes are open and they are more responsive to external stimulation. Morris and Glaser[5] have experienced a similar problem in describing the state marked by the large slow cortical activity. Following these investigators, we shall refer to the state as "dozing." It may be possible with additional monitors, especially in rhinencephalic structures, to determine if, in fact, the animals are passing through several states during these dozing periods.

The large slow cortical potentials were often replaced by spindle bursts: very rhythmic, high-amplitude activity at approximately 12 cps. This spindling invariably preceded a sleep pattern whose predominant characteristic was a marked periodicity. The very regular waves can be seen in both the ink record and the correlograms shown in Fig. XIX-12. The frequency is slightly greater than 7 cps. Another important feature of this activity is its reduced amplitude with respect to that found in the dozing animal. This pattern rarely lasted for more than 3 or 4 minutes, and was almost always terminated by movement, the movement being no more than a postural shift in most cases. Neck-muscle potentials were much smaller than those in the preceding states, averaging approximately 10 μv rms.

The potentials recorded from the anesthetized animals were very similar to those described for a number of species in which barbiturates have been employed. High-amplitude, spikelike potentials appeared at irregular intervals against a background activity of exceedingly low amplitude. The correlation analysis revealed a much lower correlation between the potentials recorded from the two hemispheres than was found in any of the normal behavioral states.

The data described above and illustrated in Fig. XIX-12 were obtained under conditions in which illumination and an acoustic noise were present in the experimental chamber. A second series of experiments in which both illumination and noise were removed yielded no consistent differences.

Thus far it has been possible to differentiate only three rather grossly different behavioral states on the basis of cortical and neck-muscle potentials. Of these, the sleep state characterized by rhythmic cortical waves is, perhaps, the most interesting. This state has several features in common with the paradoxical sleep described by Jouvet, Michel, and Coujon[10] for the cat: the reduced amplitude of cortical potentials, the low level of activity at the neck muscle, and the short duration of the state itself. The very rhythmic activity found in the rat, however, has not been described, apparently, for other species. Whether or not the resemblances are more than superficial is a question for further research. We are especially interested, too, in the possibility of obtaining a finer resolution in our measurements for the purpose of detecting smaller changes in state, particularly at the aroused end of the behavioral continuum.

A. K. Ream, R. D. Hall

References

1. J. R. Bergen, Rat electrocorticogram in relation to adrenocortical function, Am. J. Physiol. 164, 16-22 (1951).

2. R. L. Cahen, and A. Wikler, Effects of morphine on cortical electrical activity of the rat, Yale J. Biol. Med. 16, 239-243 (1944).

3. E. Girden, Electroencephalogram in curarized mammals, J. Neurophysiol. 11, 169-173 (1948).

4. D. B. Lindsley, F. W. Finger, and C. E. Henry, Some physiologic aspects of audiogenic seizures in rats, J. Neurophysiol. 5, 185-198 (1942).

5. N. R. Morris and G. H. Glaser, Effects of a pyrimidine analog, 6-azauracil, on rat electroencephalogram and maze running ability, EEG Clin. Neurophysiol. 11, 146-150 (1959).

6. M. D. Overholser, J. R. Whitley, B. L. O'Dell, and A. G. Hogan, Comparison of electroencephalographs of young rats from dams on synthetic and on normal diets, Science 111, 65-66 (1950).

7. N. Yoshii and K. Tsukiyama, Normal EEG and its development in the white rat, Japan. J. Physiol. 21, 34-38 (1951).

8. A. K. Ream, EEG Correlates of Behavioral States in the Rat, S. B. Thesis, Department of Electrical Engineering, M. I. T., June 1962.

9. J. S. Barlow and R. M. Brown, An Analog Correlator System for Brain Potentials, Technical Report 300, Research Laboratory of Electronics, M. I. T., July 14, 1955.

10. M. Jouvet, F. Michel, and J. Courjon, Sur la mise en jeu de deux mécanismes à expression électro-encéphalographique différente au cours du sommeil physiologique chez le Chat, Comptes rendus des séances de l'Académie des Sciences 248, 3043-3045 (1959).

[Editor's note: During the past nine months Dr. N. S. Sutherland, of Oxford University, has been Visiting Associate Professor in the Psychology Section of the Department of Economics and Social Science, M.I.T., and on the staff of the Center for Communication Sciences, Research Laboratory of Electronics. Sections D, E, and F that follow are special reports summarizing some of the problems on which he has been working.]

D. SHAPE RECOGNITION

a. Problems and Methods

For several years, I have been investigating the manner in which different species discriminate visually presented shapes.[1-4] The problem is to discover the physical properties or dimensions in terms of which animals classify shapes, and to infer the type of analyzing mechanism at work in the brain. Although it is impossible to specify brain mechanisms with certainty on the basis of behavioural data, the attempt is worth making because such models may have heuristic value in the collection of fresh data and although they may not be right in detail, they may at least be sufficiently close to the truth to be illuminating (cf. the Mendelian theory of genes). Moreover, if the dimensions of analysis are complex, it may be very difficult to specify them without having some model in mind.

Two behavioural methods have been used: (a) Animals are trained to distinguish between different pairs of shapes in order to establish which pairs can readily be discriminated, which are difficult or impossible to discriminate. (b) After training, animals are given "transfer tests" with other shapes in order to establish to what extent new shapes will be treated as similar to one or another of the originals. The two methods are complementary.

A simple example will demonstrate the sort of inference that it is possible to make by the use of these methods. If the primary property of shapes analyzed were the number of sides, then a square and a triangle should be easier to discriminate than a square and a diamond (method 1). Also, after training on a square and a triangle, animals should give the same response to a diamond as that which they have learned to make to a square (method 2) - in practice, animals treat a diamond as a triangle not as a square and this suggests that the number of sides (or angles) present in a shape is not one of the primary properties being analyzed.

An attempt has been made to collect data from phylogenetically different species (octopus, rat,[5,6] and goldfish) in the hope of uncovering differences in the way different animals classify shapes. If consistent differences emerge, this would provide a further clue to the dimensions under analysis and the mechanisms at work, particularly if such differences could be correlated with differences in neuroanatomy of environment. Unfortunately, work on these three species has, thus far, only established striking similarities in the way in which shapes are classified, although there are indications that

further work may uncover some differences.[6, 3, 7-12] Rudel and Teuber have recently extended this list of species and shown that some findings obtained with the octopus can be replicated in children.

b. An Early Model

In 1957, a model[1] was proposed which accounted well for many early findings. It was suggested that shapes were converted into their "horizontal" and "vertical" projections. The horizontal projection is arrived at by counting the total horizontal extent of a shape at each point on the vertical axis, and the vertical projection by counting the total vertical extent at each point on the horizontal axis. A further assumption in the model was that behaviour is more readily determined by differences in the horizontal projections of shapes than by differences in their vertical projections. This model led to many predictions most of which have been confirmed.[2] Despite its crudity, the model has proved useful in the collection of interesting and systematic data.

Amongst the earlier findings that the model predicted or explained are the following. Octopus discriminate very readily between a vertical and horizontal rectangle, but hardly at all between two rectangles, one set at 45° to horizontal, the other at 135°. The discrimination of a horizontal or vertical rectangle from an oblique rectangle is of intermediate difficulty. W and V shapes having identical projections are very difficult to discriminate; after learning to discriminate W from ⟩, animals treat ⟩ as equivalent to the original ⟩, and V as equivalent to the original W. Shapes reversed along the horizontal axis are less readily discriminable from one another than shapes reversed along the vertical axis. Two horizontal rectangles differing in length are more readily discriminated than two vertical rectangles differing in length. After being trained to discriminate a square and a vertical rectangle, they have a tendency to treat a horizontal rectangle as equivalent to the square. A square and a triangle are more readily discriminable than a diamond and a triangle. After training on square and circle, they have no tendency to treat a diamond as equivalent to the square.[2]

c. Some Recent Data

During the time that I spent at M. I. T., I analyzed some more recently collected data. This analysis indicated that the original theory was not adequate and it has suggested a new model. It is impossible to report the data in full here, but an example will make clear the sort of findings that have been obtained and what their implications are.

In one experiment, octopus were trained to discriminate between the first and last shapes shown in Fig. XIX-13. These shapes will be referred to as (Q) and (C), respectively, the letters being abbreviations for "Open" and "Closed". After training, the remaining 30 shapes were presented in transfer tests. All of the shapes were white
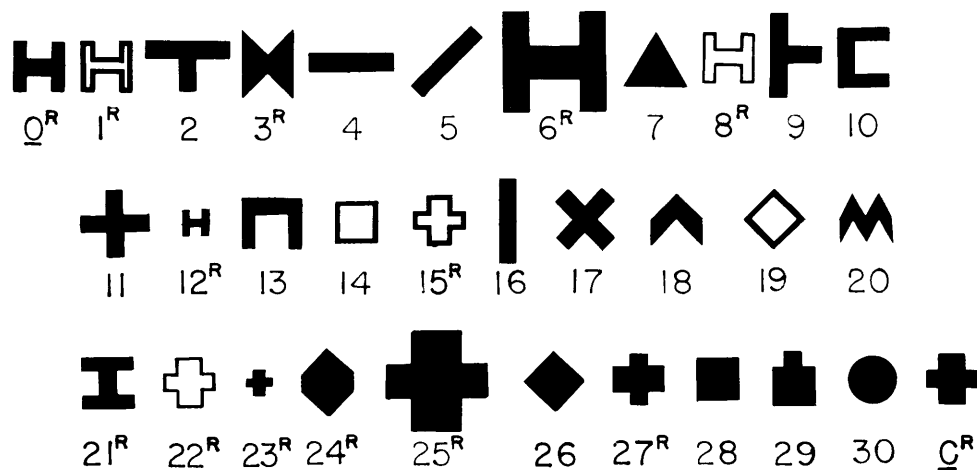
H H T M — / H ▲ H ⊢ C
Q[R] 1[R] 2 3[R] 4 5 6[R] 7 8[R] 9 10

+ H ⊓ □ ⊕ | X ∧ ◇ M
11 12[R] 13 14 15[R] 16 17 18 19 20

I ⊕ + ◆ ✚ ◆ + ■ ▲ ● +
21[R] 22[R] 23[R] 24[R] 25[R] 26 27[R] 28 29 30 C[R]

Fig. XIX-13.

except **8** and 22 which were black. For half of the animals the training shapes were 90° rotations of those shown here, and the letter "R" against a transfer shape indicates that that shape was shown rotated through 90° to these animals. The order in which the transfer shapes are drawn in Fig. XIX-13 indicates how the animals themselves treated the shapes. All shapes above rank 21 were treated as similar to the original (Q) shape and, the higher their rank, the more nearly were they equivalent to it. All shapes below 22 were treated as similar to shape (C) and, the lower their rank, the more nearly were they equivalent to it.

It will be seen that the original (Q) shape is more spread out, less compact than the original (C) shape — we shall call such spread-out shapes "open" and compact shapes "closed". There is evidence that one of the main dimensions along which octopus (and some other animals) analyze shapes is the "open-closed" dimension. It is unwise to define this too closely in the first instance, since the very problem that we are attempting to solve is to specify the physical characteristics of shapes that order them along this dimension. The reason for supposing that there is a dimension of this sort that is being analyzed is that in five other experiments in which training shapes intuitively differing along this dimension were used transfer shapes were arranged in an order very similar to that found here. Thus octopus have been trained with shapes 3 and 24,[13] shapes 11 and 28,[14] shapes 17 and 26,[14] and also with a parallelogram and a square[15]; rats have been trained with shapes 3 and 24,[9, 10] and with (Q) and (C),[8] and goldfish with shapes (Q) and (C).[11]

Before considering how far the original model can account for the position of shapes on the "open-closed" dimension, it is worth calling attention to some of the relative positions occupied by different shapes. Many of the findings are not intuitively obvious, and the data present a real challenge to explanation. In selecting findings for comment,

we shall be guided not only by their intrinsic interest but also by the degree to which they were found to be repeatable in the experiments involving training shapes other than those shown in Fig. XIX-13. Small differences in rank order are not necessarily significant on the basis of that experiment alone. The differences in the rank ordering of transfer shapes which will receive comment are those that occurred in all experiments involving those transfer shapes. When one shape is consistently found to lie nearer to the open end of the dimension than another, it will be termed the more open shape of the two. Similarly, a shape lying nearer to the closed end of the dimension will be termed the more closed shape.

Reference to Fig. XIX-13 will show that an outline of the original open shape (1) was treated in that experiment as completely equivalent to (O). There was no tendency to treat the outline of the original closed shape as similar to (C). Figure XIX-13 shows that there was actually a slight tendency to treat the outline closed shape (15) as similar to the original open shape. This finding held up in all of the other experiments. Thus even when the original open and closed training shapes were a parallelogram and a square, there was complete transfer to the outline parallelogram, no transfer to the outline square. The three rectangles are all open shapes with a horizontal rectangle being the most open, a vertical rectangle the least (shapes 4, 5, 16). A square (20) is more closed than a diamond (26), and an upright cross (11) is a more open shape than an X (17) even though in each instance one shape is simply a rotation of the other. When outline square and diamond are used, the outline square is the more open shape (14, 19). A circle (30) is the most closed shape. There is very little transfer to the rotated open shape (21). Many other shapes are treated as much more nearly equivalent to the original open shape. We must now consider how these puzzling results are to be explained.

d. The Revised Model

Many of the findings can be explained by the original model if we assume that animals are analyzing horizontal and vertical projections in terms of the number and height of the peaks present in the projection. The more peaks a shape has and the higher the peaks, the more open it is. Thus a diamond yields peaks on both projections, a square on neither, and a diamond is the more open shape. Similarly, the upright cross may be more open than an X because the former figure yields higher peaks than the latter. A horizontal rectangle yields a peak only on the more important projection (the horizontal), a vertical rectangle only on the less important projection, and again the former shape is more open than the latter. However, there are at least two findings that the original model cannot explain. (i) Since a circle yields more of a peak on both projections than a square, it should be a less closed shape than the square, whereas it is more closed. (ii) An oblique rectangle yields no peaks on either projection, but is treated as an open shape.

At the time when the original theory was proposed, there was no physiological evidence as to how the visual input was coded beyond the first few synapses. Evidence of more complex kinds of coding has recently been forthcoming from microelectrode studies on the visual cortex of the cat (Hubel and Wiesel[16]) and the tectum of the frog (Lettvin et al.[17]) Hubel and Wiesel have discovered in the striate cortex of cat neurones that have elliptical receptive fields. One type of receptive field has an excitatory centre strip running longitudinally, flanked by two longitudinal inhibitory strips. A neurone having such a field will only give a maximal response when a rectangle is laid down the length of the field covering only the excitatory centre strip. A small rotation of the rectangle abolishes the response because when the rectangle is not in the same orientation as the elliptical field, it covers both excitatory and inhibitory areas. In the cat striate cortex such neurones occur with receptive fields oriented in all visual axes. Hubel and Wiesel have discovered several other types of receptive fields, some of them considerably more complex in their properties than that described; these complex fields probably represent a further stage of analysis. It is unnecessary to describe the other receptive fields discovered in the cat; they all seem to have the property of responding maximally either to a narrow bar or to a straight edge, although some are more affected by movement of the stimulus, etc. than others.

We cannot, of course, infer from the existence of a given type of receptive field in the cat its existence in a species as phylogenetically different as the octopus. However, J. Z. Young[18] has obtained anatomical evidence suggesting that dendritic pickup fields in the optic lobe of Octopus are predominantly elliptical, and that there is a maximum number oriented in a plane that corresponds to the visual horizontal, a second maximum in the plane corresponding to the visual vertical, and fewer in intermediate orientations. It is not implausible to suggest that dendritic fields of this shape may be responsible for a similar type of coding in the octopus brain to that demonstrated as existing, by physiological techniques, in the cat. It should also be noticed that the type of analysis is not dissimilar to that suggested by Sutherland, in 1957, on the basis of behavioural evidence, although there are important differences.[1]

If we assume that in the octopus brain the counting of extents is performed by a mechanism similar to that uncovered by Hubel and Wiesel and that (following Young) there are more neurones with horizontal receptive fields than with vertical and more with vertical than with oblique, then most of the behavioural data on shape recognition in the octopus can be readily explained. It is necessary to assume only that an open shape is one that fires many receptive fields, and a closed shape one that fires few. Any thin segment of a shape will tend to fire such fields, and thin segments occur not only where a portion of a shape is rectangular or elliptical but wherever a corner occurs. We can now explain why a circle is the most closed shape, since it is without corners. A square would be less closed than a diamond, since the corners of the diamond will excite

horizontal and vertical fields, those of the square only oblique fields of which we assume there are fewer. Since the corners of the triangle are more acute than those of the diamond, it will be a more open figure. The horizontal rectangle will still be an open shape. Outline shapes will be more open than the corresponding filled-in shapes.

It is clear that the remaining data summarized above can be accounted for in similar ways. It is necessary to assume that as well as a count of the total number of neurones excited (giving the position of a shape on the open-closed dimension), an analysis is also performed of proportions fired with fields in different orientations. This second type of analysis would account for much of the earlier data. Moreover, even when training shapes do differ on the "open-closed" dimension there is evidence that transfer is determined to some extent by whether the orientation of thin segments in transfer shapes is the same as or different from that of the segments of the open training shape.

It has only been possible to give the barest outline of a new model here, and clearly a great deal of further work remains to be done in order to test and develop it. For example, in order to account in detail for the ordering of transfer shapes, it would be necessary to optimize various parameters of the model such as the actual widths and lengths of the fields (in terms of visual angle), and the ratio of fields in one orientation to fields in other orientations. This could be achieved by means of a computer program, and the existing behavioural data are sufficiently extensive to evaluate the goodness of fit which resulted after optimization. Final corroboration (or disproof) of the model must, of course, await more detailed physiological studies on the visual system of Octopus such as may be forthcoming when J. Y. Lettvin is able to resume his micro-electrode work on the optic lobe. In the meantime, the behavioural data represent a challenge to neuroanatomy and physiology and may be useful in suggesting the type of organization to look for.

e. Subsidiary Findings

Other recently analyzed results are relevant to a subsidiary aspect of shape discrimination. It has been found that within the size range used the larger the training shapes, the more readily discriminable they are.[10] In transfer tests there is always more transfer to larger versions of the original shapes than to smaller (cf. Fig. XIX-13, shapes 6, 12, 23, 25). This is not due to a limitation set by peripheral acuity.[19, 20] Single horizontal and vertical rectangles measuring 5 cm X 1 cm are difficult for octopus to discriminate from one another. However, if two patterns with a square outline are made up, one from 20 black and white vertical rectangles, the other from 20 horizontal rectangles, these patterns of reduplicated rectangles are very easily discriminated.[21] This finding is readily interpretable in terms of the Hubel and Wiesel results, since many more receptive fields in a given orientation will be fired by a pattern of reduplicated rectangles than by a single rectangle, and it should be correspondingly

easier for detection mechanisms to pick out the differences in firing patterns resulting from presentation of the two shapes.

N. S. Sutherland

References

1. N. S. Sutherland, Visual discrimination of orientation and shape by Octopus, Nature 179, 11-13 (1957).

2. N. S. Sutherland, Theories of shape discrimination in Octopus, Nature 168, 840-844 (1960).

3. N. S. Sutherland, The methods and findings of experiments on the visual discrimination of shape by animals, Quart. J. Exptl. Psychol., Monogr. 1, 1961.

4. N. S. Sutherland, N. J. Mackintosh, and J. Mackintosh, The relative importance of horizontal and vertical extents in shape discrimination by Octopus (in preparation).

5. N. S. Sutherland, A. E. Carr, and J. Mackintosh, Visual discrimination of open and closed shapes by rats. I. Training (Quart. J. Expt. Psychol., in press).

6. N. S. Sutherland, Visual discrimination of horizontal and vertical rectangles by rats on a new discrimination training apparatus, Quart. J. Exptl. Psychol. 13, 117-121 (1961).

7. N. S. Sutherland, The discrimination of shape by rats: squares and rectangles (in preparation).

8. N. S. Sutherland, A further experiment on the discrimination of open and closed forms by rats (in preparation).

9. N. S. Sutherland and A. E. Carr, Visual discrimination of open and closed shapes by rats. II. Transfer Tests (Quart. J. Exptl. Psychol., in press).

10. N. S. Sutherland and A. E. Carr, The visual discrimination of shape by Octopus: the effects of stimulus size (Quart. J. Exptl. Psychol., in press).

11. N. S. Sutherland and J. Mackintosh, Visual discrimination by goldfish: The orientation of rectangles (in preparation).

12. N. S. Sutherland and J. Mackintosh, The visual discrimination of open and closed forms by goldfish (in preparation).

13. N. S. Sutherland, Visual discrimination of shape by Octopus: Open and closed forms, J. Comp. Physiol. Psychol. 53, 104-112 (1960).

14. N. S. Sutherland Visual discrimination of shape by Octopus: Squares and crosses (J. Comp. Physiol. Psychol., in press).

15. N. S. Sutherland, N. J. Mackintosh, and J. Mackintosh, Visual discrimination of shape by Octopus: Squares and parallelograms (in preparation).

16. D. H. Hubel and T. N. Wiesel, Receptive fields of single neurons in the cats' striate cortex, J. Physiol. 148, 574-591 (1959).

17. J. Y. Lettvin, H. R. Maturana, W. S. McCollough, and W. H. Pitts, What the frog's eye tells the frog's brain, Proc. IRE 47, 1940-1951 (1959).

18. J. Z. Young, Regularities in the retina and optic lobes of Octopus in relation to form discrimination, Nature 186, 836-839 (1960).

19. N. S. Sutherland, The discrimination of stationary shapes by Octopus: Further open and closed forms (Am. J. Psychol., in press).

20. N. S. Sutherland, Visual acuity and discrimination of stripe widths in Octopus vulgaris Lamarck (Pubbl. Staz. Zool. Napoli., in press).

21. N. S. Sutherland, J. Mackintosh, and N. J. Mackintosh, The visual discrimination of reduplicated patterns by Octopus (in preparation).

E. SWITCHING-IN STIMULUS ANALYZING MECHANISMS

Results have been analyzed and papers have been written during the past nine months which are relevant to a second issue. The problem discussed in Section XIX-D was studied to specify the stimulus-analyzing mechanisms for visually presented shapes. The second problem is to determine how different analyzing mechanisms interact in the learning process. I suggested that discrimination learning involves two processes.[1,2] First, animals have to learn which stimulus-analyzing mechanism to select: They must switch-in that mechanism that yields different outputs for the two stimuli that are to be discriminated. If an animal is being trained to discriminate a white horizontal rectangle from a white vertical rectangle, it cannot learn the discrimination if it switches-in only a mechanism that analyzes the brightness of the shapes. Second, the animal must learn to attach the correct responses to the outputs from the selected analyzer. The two processes will, of course, overlap in time, although they may be mediated by discrete mechanisms in the nervous system. If we assume that the time course of the two processes is different, and that it takes longer to switch-in an analyzing mechanism firmly than to attach the correct responses to the analyzer when it is selected, then it is possible to explain some paradoxical findings that are already well established.

The more training an animal receives on a given discrimination, the faster it learns to reverse it, i.e., the more an animal is trained to select stimulus A and avoid B, the faster it subsequently learns to select B and avoid A. This finding follows from this model: The effect of prolonging training on the original discrimination will be to switch-in the analyzing mechanism more firmly so that the overtrained animal when faced with the reversal problem will keep the right analyzing mechanism switched-in and will have a chance to learn to reverse its responses. The nonovertrained animal, not having learned to switch-in the original analyzing mechanism so firmly, will try out other analyzers and as long as it does so cannot learn to reverse its responses to the outputs from the appropriate one. If this is the correct explanation of the effect of overtraining on reversal, it follows that animals taught one discrimination and then required to learn a completely different discrimination should be retarded on the second problem by overtraining on the first. The overtraining will now switch-in more firmly the wrong analyzing mechanism instead of the right one. The first experiment to test the model confirmed this prediction. It was conducted on the rat by N. J. Mackintosh[3] of Oxford University, and he has since derived and tested many other predictions. His

work will not be summarized here.

Our model explains a second paradoxical finding. If an animal is required to discriminate two stimuli lying very close together on a dimension, total learning time is much less if the animal is first trained with two stimuli lying far apart on the dimension and then trained in succession with stimuli lying closer and closer together than if it is trained from the outset on the difficult stimuli. According to our model, an animal that is being trained with stimuli differing little from one another should have difficulty finding the correct analyzing mechanism because even when the correct analyzer is selected mistakes will still be made, owing to overlap in its outputs caused by the fact that the stimuli lie very close together on the relevant dimension. A recent experiment[4] on octopus established three findings that are in line with the theory. All animals were trained to discriminate between a square and a parallelogram, but the similarity of the shapes that were being discriminated was varied by using parallelograms whose angles differed from 90° by various amounts. (i) Animals first trained on parallelograms differing widely from a square subsequently performed more accurately with a parallelogram differing very little from the square than did animals that were given the same total number of training trials with the latter parallelogram. (ii) Animals trained from the outset on the most difficult parallelogram performed much better when subsequently they were shown a square and a parallelogram differing widely from it than they had been performing on the original discrimination, although they were given no opportunity to relearn the second discrimination. This suggests that these animals were using the correct analyzing mechanism on some trials, and that with the difficult shapes they were making two types of mistake: on some trials the wrong analyzer was selected, and on others, although the right mechanism was selected, its outputs overlapped. The second class of error was reduced when a parallelogram differing more widely from the square was presented. (iii) Different animals were trained with both shapes shown at once and with each shape shown singly on separate trials. The performance of the two groups was the same when a parallelogram differing widely from a square was used, but the performance of animals who saw both shapes at once was far superior when the discrimination was difficult. The effects of noise in the analyzing mechanism were unimportant when the shapes used differed widely, but they became important when the discrimination was difficult. Difficult discriminations are better performed when both shapes are presented simultaneously because then it is not necessary to store an absolute quantity in the nervous system and because although noise in the analyzer will affect the absolute outputs for both shapes, it will affect the relative outputs less when both shapes are shown simultaneously.

A second experiment[5] on octopus established that by pretraining with stimuli differing in shape, it was possible to switch-in an analyzer that was sensitive to shape differences which subsequently remained switched-in when animals were faced with a problem that

could be solved either in terms of shape or size, or both. Animals pretrained to respond in terms of shape learned very much more about shape at the second stage than did animals pretrained to respond in terms of size.

Our model has been presented in an oversimplified form. It is not necessary to assume that only one analyzer can be used at a particular time, only that at any given time behaviour tends to be more influenced by the outputs from some analyzers than by the outputs from others. Apart from explaining the evidence already cited, this model may help in the understanding of a much wider range of phenomena. For example, it has long been known that attention is selective and that it is difficult or impossible to perform two tasks at once. The model also has implications for work on automata and for neurophysiology. If the same operation has to be performed on a number of different inputs (e.g., inputs from different modalities), it would clearly be economical in terms of brain tissue to use one mechanism to perform that operation rather than to duplicate the mechanism for parallel information channels. It is likely that there are control centers in the brain which select sequential operations to be performed on the inputs. Depending on the operations selected and their sequence, one would thus be able to discriminate along a large number of dimensions without a great reduplication of mechanisms, although one would not be able to discriminate along a large number of dimensions simultaneously. It seems likely that some of the routing of the inputs may be controlled by efferent fibres known to exist in several sensory pathways.

A comparative approach has again been used in the study of the present problem, and it appears that many of the same phenomena that we attribute to the switching-in of analyzing mechanisms are present in both rat and octopus. This fact gains significance when we recall that these species are widely separated in phylogeny and that the phenomena in question are not exhibited by any existing automata.

N. S. Sutherland

References

1. N. S. Sutherland, Stimulus analysing mechanisms, Proc. Symposium on the Mechanization of Thought Processes, Vol. II, pp. 575-609 (H. M. S. O. London, 1959).

2. N. S. Sutherland, Switching in stimulus analysing mechanisms, Proc. Third ONR Symposium on Physiological Psychology, 1962 (in press).

3. N. J. Mackintosh, The effects of irrelevant cues on a reversal and non-reversal switch (J. Comp. Physiol. Psychol., in press).

4; N. S. Sutherland, N. J. Mackintosh, and J. Mackintosh, Simultaneous discrimination training of Octopus and transfer of discrimination along a continuum (J. Comp. Physiol. Psychol., in press).

5. N. S. Sutherland, N. J. Mackintosh, and J. Mackintosh, Shape and size discrimination in Octopus: The effects of pretraining along different dimensions (in preparation).

F. RECOGNITION, RECALL, AND INFORMATION

It has commonly been supposed that recognition is easier than recall. Subjects make fewer mistakes when asked to recognize items than when asked to recall them. However, in most recognition tasks the ensemble from which the subject has to select is smaller than in recall. It follows that if subjects made the same number of mistakes in the two tasks, they would actually be transmitting more information in recall than in recognition. I have previously suggested[1] that subjects might, in fact, transmit the same amount of information in both tasks, and that the greater number of errors made in recall might simply be a consequence of the larger ensemble from which selection is made. In order to test this hypothesis, it was necessary to develop a method of measuring the information transmitted in the two tasks.

In recognition, subjects only convey information about what items are in the list that is sent: No information is transmitted about serial order. We therefore needed a method of measuring the information conveyed by transmitting items from a list without regard to their order of occurrence: This has been termed "what" information. Except in the case for which there is no loss of information in transmission, the number of correct choices made by a subject will vary from trial to trial. It turns out that in order to obtain a direct estimate of information that is being transmitted in these tasks, we would need an impossibly large number of trials. We were able to circumvent this problem by developing a method for measuring information transmitted by any subject whose average number of correct responses per trial are known. We shall call this number s, and let S be the actual number correct on a given trial. The chance distribution of S can be calculated for a given ensemble size and for a given number of items sent and a given number of items received. By a minimization procedure involving the use of Lagrange's method of undetermined multipliers, it is possible to calculate the distribution of S for a given s value under the assumption that S will be random with the constraint that s is fixed. From the distribution of S thus obtained we can calculate the amount of information that is being transmitted.[2]

In investigating problems of recall, it would be of considerable value to be able to estimate not only "what" information but also "order" information. By "order" information is meant the information conveyed by the order in which items are selected when no information is conveyed by what the items are. In concrete terms, we wish to compare the amount of information transmitted when a subject has to memorize items without regard to their order with the amount transmitted when a subject already knows what the items are but has to memorize their order. This approach should throw light on storage mechanisms in the brain. For instance, we can compare the efficiency of storing symbols in different locations with the efficiency of ordering symbols already stored.

The problem of finding a method to measure "order" information independently of "what" information was solved during my stay at M.I.T. Just as in the case of "what" information, it is, in practice, impossible to measure "order" information directly, since an impossibly large number of trials would be involved. The difficulty is to find a quantity S' that measures the correspondence between two orderings and has a chance distribution that can be determined. Kendall[3] has developed just such a measure for another purpose, and, by chance, also labelled it S. Kendall's S represents the first stage in calculating the rank order coefficient τ, and is a measure of the correlation between two orderings with a known distribution. To distinguish this measure from the S used in determining "what" information, let us call it S'. Since the distribution of S' is known, we can again minimize S' with the constraint that its average value s' is fixed, and it is then possible to compute the amount of order information transmitted for a given value of s'. The latter value can be readily determined experimentally for a given subject under a given set of conditions. To calculate the information trans-mitted for different values of s, a computer program was written and executed on an IBM 709 computer in the Cooperative Computing Laboratory, M.I.T. Some experiments will soon be conducted in which the results will be used to estimate the amount of "order" information transmitted under different conditions.

The author was responsible for the basic ideas underlying this work and for the programming. He wishes to acknowledge the work of Dr. B. R. Judd of the Radiation Laboratory, University of California, Berkeley, who set up the mathematical equations involved in the minimization procedure.

<div align="right">N. S. Sutherland</div>

References

1. R. Davis, N. S. Sutherland, and B. R. Judd, Information content in recognition and recall, J. Exptl. Psychol. 61, 422-429 (1961).

2. B. R. Judd and N. S. Sutherland, Information theory and nonsequential messages. Information and Control 2, 315-332 (1959).

3. M. G. Kendall, Rank Correlation Methods (Griffin, London, 1948).