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CORRELATIONS BETWEEN CORTICAL NEUROPHYSIOLOGICAL
ACTIVITY AND SHORT-TERM BEHAVIOR IN THE MONKEY

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One of the problems posed by this Symposium seems to involve an appalling task--the correlation of neurophysiological activity in the brain, the structure, the total behavior, and, presumably, the subjective activity within each animal. If one takes a very close look at the data obtained in the fields of research dealing separately with these four aspects, one is overwhelmed by the missing parts in each separate picture and impressed by the lack of correlatable data taken with individual animals simultaneously in the four areas. Obviously, subjective reports are available at present only from human subjects. Some limited data are being obtained from the human in a number of clinics (3, 4, 6), but the scientific usefulness of these data is questionable because of the limitations of the methods used (anatomical, for example). In my opinion, theories to bridge the fields and fill the gaps in our data within each field are almost useless: The next collector of data can restore the status of the gaps by merely filling in the edges a little more. Instead of theories, we need more data--taken with methods at hand and with new methods being developed.

The anesthetized central nervous system or the partially ablated central nervous system is, for all practical considerations, the classical preparation of electro-neurophysiology. The intact, boxed up, whole animal is the classical preparation

of experimental psychology. In recent years there has been a movement in physiology to use unanesthetized animals and in psychology, to use stimulation with electrode implants in the relatively intact animal. Workers in each field are invading the other field, at least methodologically, and sometimes by coöperative effort. We come from the physiological side and intend penetrating into the psychological territory but with physiological weapons and intentions.

One of the big gaps in our knowledge, not filled by either physiology or by psychology, is an accurate time-space description of central nervous system electrical activity and behavior in the very short time-intervals. Psychologists tend to deal with long cumulative phenomena, the results of many billions of short-term events. The classical learning-motivation-drive studies illustrate the point; even perceptual-discrimination-motor-response experiments involve a long-term, complex spatial-temporal sequence of stimuli of unending variety from one milli-second to the next; such experiments also bring in long chains of multiple, interlocked behavioral continua lasting seconds to minutes, repeated in complex variety over hours and days and weeks. Such studies generate repeatable patterns for each species which can be described and pinned down as "laws" couched in statistical terms.

Physiologists tend to investigate CNS events which occur in intervals of time of microseconds to tens of seconds and of short-term behavior of comparable time-spans (called "movements," "arousal," or "autonomic responses"). If a physiologist

wishes to deal with the field of learning or drive, he contemplates the long and laborious task of analyzing a learning sequence. He sees that there are 3,600,000 msec. in every hour and several hundreds of millions of neurons, each of which is significantly active in one way or another at least several times per second; he can fairly easily record the activity of, and influence the action of, parts of groups of fifty thousand or so neurons at a time, and he can seek repeatable patterns lasting tenths of seconds to seconds. It may be that clues to CNS learning mechanisms can be found in such patterns; it may be profitable to hunt during a learning situation, for changes in such patterns during the time necessary for learning to take place, in new distributions of such patterns, and in the large field of that which we, in our ignorance, call "spontaneous" activity. Such studies on the detailed mechanisms of learning assume that one can see statistically significant short-term patterns or modulations of patterns in the CNS activity of an unanesthetized animal, patterns related to sensory events ("evoked responses"), to movements ("motor responses"), and to integrative events. We have been studying the evoked responses and the elicitable movements in unanesthetized monkey's cerebral cortex; our first problem has been to relate the findings in the unanesthetized brain to those found in the anesthetized one. In brief, on the motor side the patterns are similar with a few important differences; on the sensory side there are distinctive differences, mainly with respect to the much larger cortical areas over which responses

can be seen, and in respect to the animal's external environment which is necessary to see any responses at all.

As far as integrative events are concerned, we do not yet have a clear picture of how much of what we traditionally include under "sensory," "motor," or "spontaneous" activities are truly integrative. We suspect that if we can separate out the strictly repeatable and stereotyped activities from the more fluid, plastic, modifiable ones, we can at least distinguish that which the monkey's brain has already acquired (by learning or other processes) from that which it can yet acquire in a new conditioning or learning situation. It is these repeatable patterns that we have been exploring to date; the conditioning experiments will come later, when we understand something of the more or less fixed parts of the CNS patterns; these parts may be modifiable, but we need to know more of how fixed they are under a variety of conditions.

In working with unanesthetized monkeys we found that which is already probably obvious to psychologists: Monkeys are not only distractable, but can be intractable. They are extremely sensitive, affectionate, curious, active, and responsive, and they learn rapidly the limits of restraint. When a monkey is stimulated through implanted electrodes on the cortex, one can see repeatable movements only with the cooperation of the monkey; this procedure takes unending patience--each monkey has its own ways of foiling our aim of repeatability, and most monkeys become impatient when one part of the body moves again

and again in the same way. Despite these difficulties, given weeks of time to work on the same animal, one can obtain a fair picture of evocable short-term motor movements tied to the stimulus parameters and the locus stimulated. A large fraction of the time, a pattern of movement is so tied to the stimulus that even naive visitors can see it superimposed and standing out from the noisy background. This situation is far better than that for observing the electrical activity within the CNS: In this latter case, there are fewer patterns that one can see, much less record, in the background in a noisy environment.

The external conditions under which one can record repeatable CNS patterns is reminiscent of the Pavlovian camera: The animal must be isolated from all distracting stimuli, even very weak ones. The subsonic vibrations in the laboratory because of a streetcar moving two blocks from the building at 3 A.M. have destroyed the reproducibility of responses. There are a few exceptions to this rule: If a voluntary movement is violent enough, one can see related, repeatable patterns in the CNS, but even these require special means for detection. We find that the visualization of the activity of many zones at once, so that one can see the instantaneous relations among the activities of these zones, to be the important set of variables if we are to see the patterns related to the movement. We have tried the usual ink-writers and oscilloscopes, but among all the bumps and hollows of the record, one is quickly lost--it is the difference between walking over a terrain and moving above it and looking down on it. The ink-writer carries

one through every rise and fall; the instantaneous viewer (bavatron [10]) gives one a look at the relations between neighboring rises and falls, so that one can see the patterns of the surface. Or, to emphasize the point further, it is the difference between viewing the video signal of a television station with a very high-speed ink-writer and viewing a proper receiver with the traces placed in their proper places in sequence; it is not very easy to reconstruct the moving images from the ink-written amplitude record alone.

In order to start on the trek toward the psychological side with unanesthetized animals, in 1949 we started implanting arrays of pickup and stimulating electrodes on the pial surface of the monkey's cortex. The site was chosen because it was thought that the alternative, penetrating electrodes may give a picture contaminated by the activities of damaged cell groups; a "normal" physiological baseline was needed first in order to quantify possible pathological activity caused by penetration. The first arrays contained 25 electrodes; later ones contain 29, 36, and 121 electrodes covering 1 sq. cm. of cortex. Our latest monkey has 610 electrodes implanted over approximately 19 sq. cm. of cortex at about 1.5- to 2-mm. intervals over one hemisphere (30 electrodes/cm²) (Fig. 1.)

The method of picking up and recording the electrical activity is designed to present and to record through 25 channels in a square array 5 by 5, maintaining the spatial relations on the cortical surface in the final record (10, 13).

At present we are limited to simultaneous data from any 25 electrodes in our present array of 610.

The method of restraint of the monkey to prevent self-inflicted damage to the head has been evolving slowly. It started with a table with a hole for the head and a suspended seat, and an additional Lucite sheet was added over the lap; the size was finally doubled as we began to use fully matured monkeys. We are still not satisfied with this method--some movements are impeded too much. Lately we have been trying some new arrangements, none of which are completely satisfactory.

CNS STIMULATION

Electrical stimulation of brain activity has posed several problems: Our aim has been to use stimuli patterned spatially as well as temporally, but many preliminary experiments must be completed before such "spatial" stimulation can be accomplished. In order to do this over long periods of time through many electrodes, it has been thought necessary to find a waveform which excites in a brief time (less than 0.5 msec.) and which does not injure neurons when used for many hours per day for several weeks. The brevity of the excitation period for each pulse is necessary for fine control of neuron populations near each electrode by amplitude and/or frequency modulation of the stimulating pulse trains; as one decreases pulse duration, one finds an increasing range of amplitudes at a given frequency between just-threshold effects and full, violent local afterdischarge patterns, and in increasing change

of threshold with changes in frequency of the pulse repetition rate (14, 17). Rectangular unidirectional pulses were used and discarded because they were found to be injurious (14, 18). Symmetrical brief bidirectional pulse-pairs offer a noninjurious stimulus for one solution to the stimulation problem (17); if both pulses are brief enough, they cause minimal artifact and allow simultaneous stimulation and recording in nearby areas.

In order to use spatially patterned stimuli within the brain, it is convenient to know what responses are produced by stimulation through single electrodes when used without the others; such trains of stimuli, introduced through single electrodes, produce test spots of hypersynchronized, more or less controlled activity within the CNS and cause small stereotyped patterns of behavior for short time-intervals; with such stimuli, we see the results of single hypersynchronized fractions of groups of fifty thousand or so cells. To obtain threshold excitation of such cortical spots, more than one pulse-pair is needed; and the threshold is a function of the number of pulse-pairs, the frequency, and the duration of the train. Trains have been found to be necessary for build-up of most motor responses (14, 17). Trains in the region of 60 pulse-pairs per second evoke the classical type of motor map; low-frequency pulses of about 2 per second give the Liddell and Phillips type of map (9).

In anesthetized monkeys, extensive areas of cortex have been shown to produce specific movements: Horsley and Schäfer (7) found pre- and postcentral somatic areas; Woolsey,

et al. (25) showed the detail on the precentral gyrus; W. K. Smith (22) and R. B. Livingston (19) mapped the anterior eye fields; Walker and Weaver (23) demonstrated the existence of some of the posterior eye fields; Bechterew (2) found a temporal ear field.

With implanted arrays in six monkeys, we found that those same areas of cortex produce very similar movements in the unanesthetized monkey (Fig. 2) (12).

The maps of the movements elicitable from most of the lateral convexity of the hemisphere in an unanesthetized monkey with 610 implanted electrodes, have been completed and checked in detail over a period of eight weeks; there are no gaps in the maps over the hemisphere from the lateral to the medial borders and from the frontal pole to the occipital areas. At low frequencies, lip, tongue, leg, tail, and ear are found, but thumb and fingers respond over most of the area (Fig 3) (9). At higher frequencies (Fig 4), coördinated eye and head movements occur in extensive frontal, occipital, and temporal regions; arm and hand movements over a very extensive precentral-parietal region; leg, over a more medial region of the precentral-parietal cortex. Face, lips, and tongue are found laterally over precentral-parietal cortex, and ear movements in frontal cortex and over that which we estimate to be near or on temporal acoustic cortex (20).

This map confirms the work of others mentioned above on anesthetized animals. In addition, the anterior eye fields

are found to extend to the frontal pole. These results demonstrate that once the variable depth of anesthesia is abolished, most, if not all, cortical areas have motor connections in quite detailed and specific ways. Contrary to the expectations of some workers (25), the maps are stable and easily elicitable in the unanesthetized monkey; by judicious procedures, the level of excitability from animal to animal can be held constant.

The area given to movements of the spinal column also gives bilateral limb movements. The area corresponds closely to that for "back" in the anesthetized animal (25). Stimulation here causes rather surprising activation of the whole monkey; it seems to be very much aroused when we work with this region; in contrast with other regions, the monkey does not doze as long as stimuli enter here. The movements elicited are rather striking; for example, at one electrode, we found a movement we call "shrink," which consists of complete pulling-together of the contralateral pinna and closure of the external auditory meatus, tight closure of the contralateral eye, pulling of the head to the ipsilateral side, and raising and flexing of the contralateral arm--all as if to ward off and "shrink" from a blow to the contralateral side of the head. At an adjacent electrode we found a pattern called "goose"; this pattern involves the whole body, and the reaction looks as if the monkey had been forcefully, mechanically stimulated par anum. (Apparently this region corresponds to part of area "4S" and can cause "activation" rather than the "suppression"

one might expect from the work of Dusser de Barenne and McCulloch [5].) Some pre-emptive evidence from electrical responses picked up from this region, evoked by stimulating other regions electrically, suggests that this small area has extensive inputs from the whole large "arm" and "leg" area. The "hyper-arousal" effect suggests it has efferents to the subcortical "arousal" systems (see H.W. Magoun's contribution to this Volume).

Taken as a whole, this "motor cortex" map suggests at least two "motor monkeys" (simiusculi [25]): the anterior one of Woolsey et al. (25), facing forward and down with legs up and back, but including eyes anterior to arcuate sulcus, and one posterior with eyes looking aft, whose orientation is still not thoroughly worked out; if its "spine" is not found postcentrally, a major reinterpretation of these simiusculi is then possible.

We have, as yet, no direct evidence as to how such an extensive area as this surface of the hemisphere can connect directly or indirectly with anterior horn cells of the cranial and spinal motor nerves. Theoretically, many main pathways, including the pyramidal one, are activated. It seems rather surprising that we did not obtain more widespread bilateral movements in the absence of anesthesia. We found some around the "spine" region, and, as did Woolsey et al. (25), some in the far lateral mouth area; apparently the commissural connections do not have an extensive and important role in cortical efferent activity. Perhaps both hemispheres are more cooperative

than slavish in their relations. Of course, "eyes" are a special case.

From the behavior of the monkey, it can be deduced that somatic sensory events may have a lower threshold post-centrally than the motor responses; a few percentage points below the threshold for movement, the monkey may move around uneasily during the train, scratch at the part which moves at higher currents, or carefully inspect the part visually. We call such behavior "reactions to sensory responses" to separate them from the more stereotyped motor responses.

In terms of behavior, it may not be surprising to find such large cortical areas implicated in arm and hand and eye movements in the monkey. It does use eyes and hands extensively in its usual way of life in quite specific, integrated, and complex patterns of behavior. It is probable that the "sensory" inputs and the "motor" outputs are computed here in ways yet to be determined. Since we feel that these results are to be attributed more to the "superb architect" and less to the "sloppy workman" of Huggins and Licklider (8), we have done some preliminary analyses of the areas of these maps and their relationships.

Adrian (1) suggested that the scale of the somato-sensory map of a given peripheral area mapped on cortex is closely related to the necessity of detailed information from that part of the periphery used most often in the behavior of the animal. It has long been suspected that the scale of the movement-muscle map is closely related to the frequency of use

and the necessity of detailed and multidirectional control of positions and movements of the peripheral part.

The use of one part depends on that of others: the use of the fingers and the hand depends on that of the arm, and the arm on that of the shoulder and spine. On the cortex, "spine" is very small and lies in the large "shoulder" area and between "arm" and "leg"; "shoulder" is small and lies in the larger "arm" area, which, in turn, lies in the larger "hand" area; therefore, we call the hand-arm-shoulder a functional group represented as a unit on the cortex; "spine" is related also to "leg" and, as stated above, is a special region also related to many deep systems. All the large group of body parts thus can be divided, motor-wise, into functional groups: hand-arm-shoulder, eyes-head, spine, foot-leg-hip, tongue-lips-jaw, and ear. (The latter one probably should be "ear-head".) The corresponding cortical areas show extensive, if not complete, overlap of parts within each group. With this division we find, on the available cortical surface, the cortical areas to be those given in Table 1.

Table 1 Superficial area on lateral convexity of one hemisphere for movement of given parts

Movement of	Number of Electrodes	Estimated area cm. ²	Fraction of total area observed
Hand-Arm-Shoulder	294	9.80	0.38
Eyes-Head	267	8.90	0.34
Foot-Leg-Hip	84	2.80	0.11
Tongue-Lips-Jaw	62	2.07	0.08
Ear	50	1.67	0.06
Spine	26	0.87	0.03

The areas found are only minimal values: cortex in sulci, and beyond our array, contributes additional area to at least some of these groups. We estimate that the "eyes-head" area will be sizably increased when we can explore the depths of the lunate sulcus and the rest of the occipital and temporal lobes. We do not expect "hand-arm-shoulder" to be as greatly increased as "eyes-head." A large fraction of this area is already bounded on our present map, and the supplementary and secondary motor areas are relatively small. "Leg" will probably be sizably increased when the medial cortex is explored (25). Allowing for such probable additions for each group, we guess that the order of the areas will be shown to be that of Table 2. Careful quantitative studies of total macaque

Table 2 Presumed rank of given functional units by

Total cortical area	
Area rank	Functional unit
1.	Eyes-Head
2.	Hand-Arm-Shoulder
3.	{Foot-Leg-Hip {Tongue-Lips-Jaw
4.	Spine

behavior may reveal the exact relations of the use of these groups and these cortical quantities. Naturalistic observations suggest that the behavioral frequency-of-use rank order is very close to this cortical-area rank order. The monkey appears to "lead with its eyes" in most situations, and get

busy with its hands almost as frequently--when it is eating, its eyes, hands, and mouth are very busy; when climbing, its hands and feet are very busy.

Overlap of the cortical maps for these groups and the lengths of the boundaries between them, may be related to their necessary behavioral relations: Table 3 gives this rank order

Table 3 Relations between cortical representatives of parts

Rank order	Cortical overlap and borders between
1.	"Eyes-Head" and "Hand-Arm-Shoulder"
2.	"Hand-Arm-Shoulder" and "Foot-Leg-Hip"
3.	{ "Eyes-Head" and "Ear-Head" "Hand-Arm-Shoulder" and "Tongue-Lips-Jaw"
4.	"Hand-Arm-Shoulder" and "Spine"
5.	"Eyes-Head" and "Foot-Leg-Hip"

from the map. These results neglect buried cortex and cortex outside the array. When other cortex is explored, we estimate that this rank order will not change very much--but we will be able to add the lower-order relations about parts which have only small areas on this lateral convexity of the hemisphere. We eliminated from Table 3 all parts with fewer than ten electrodes on borders or overlaps. Referring again to the naturalistic picture of monkey behavior, eyes-hand relations seem to be dominant and have the finest detail of spatial control in three dimensions: binocular visual fields and target-seeking behavior of eyes and head, and searching, picking,

probing, grooming, lifting, and grasping with hands are two interlocked sets of relations presumably needing large areas of cortex and large areas of border and overlap. Feeding and grooming take up some of the hand and mouth relations, etc.

We have been intrigued by the question of what is missing from this movement map--apparently a large amount of basic facial and vocal expression is yet to be found, and may exist in regions outside our present array, deeply, laterally, and/or medially.

In our series of stimulated monkeys, including Susie with the 610 electrodes, we have found that the threshold current for movement, at any one locus, varies with the state of the animal. There are short-term variations, depending on the just-previous stimuli and on voluntary movements and inhibitions of movements by the monkey itself (wherever it is in the CNS!); in electromyographic records, we see waxing and waning of the amplitude over periods of 5 to 10 sec. or less (Fig. 5). High-frequency, subthreshold trains of electrical stimuli can decrease, briefly, and then increase strongly the amplitude of subsequent responses for up to 30 sec. later (Fig. 6) ("prolonged facilitation" of Larrabee and Bronk; "post-tetanic potentiation" of Lloyd).

Longer-term variations in threshold are seen with dozing, sleeping, and eating. Dozing and sleep raise the threshold 25 to 100 per cent above that of the awake state. About $\frac{1}{2}$ to 1 hr. after eating, there is a small (15 to 25 per cent) fall in threshold (Fig. 7).

I cite these facts as a reminder that the unanesthetized CNS is complex and constantly in need of careful and close observation to account for its apparent "instability." Instead of being "instable," however, it seems to take facts into account which, as yet, are not fully available to us.

We find, as did James W. Ward (24) in unanesthetized cats, that what the monkey is doing has something to do with the movement elicited by the electric current (but we do not yet agree with his "common final position" interpretation). If we work with a cortical zone that gives progressing "elbow flexion" when the arm is relaxed and extended, and persist long enough, the monkey may get tired of this game and voluntarily flex its elbow strongly enough to stop our efforts. At that point, we see progressing relaxation of the biceps in response to our stimuli. Similarly, if the response is "eyes and head turning to the contralateral side," the monkey may stare at something ipsilateral and raise the apparent threshold; but if it loses interest, the eyes start moving contralaterally. Once in a while we see a "nystagmoid" series of eye movements as the monkey pushes one way and the stimulus pushes the other.

When I say "it pushes" or "it does this," I am taking the "common sense" view of the situation. If one works in close quarters with these beasts for several weeks, one develops the feeling there is someone in the unstimulated majority of that body-brain either aiding or hindering the experiments, a someone whose efforts are not usually seen in a Skinner Box.

CNS ELECTRICAL ACTIVITY

With the method of recording from 25 electrodes at once, the electrical activity can be seen to be traveling waves of "figures" (11, 13, 15, 16). These figures differ from one cortical area to the next and are different for responses to normal inputs (ear, eye, etc.) and for "spontaneous" activity. In the cat's acoustic (AI and AII) cortex and the posterior ectosylvian field (Ep) of Jerzy Rose (21), the differences between evoked figures and spontaneous ones are particularly striking (Fig.8) (15, 16). A figure, evoked by a click, starts in AI and AII and grows with an advancing edge velocity of 1 to 2 m/sec; at the boundary with Ep, the edge slows to 0.1 m/sec. The retreating edge velocity over the whole area is about 0.1 m/sec.

The spontaneous figures usually arise in Ep just posterior to the AI-Ep boundary or at a locus near the posterior suprasylvian sulcus. The velocity of the advancing and retreating edges of these figures is about 0.1 m/sec. These figures in Ep can excite new ones in AII and in turn can be stimulated by "startling" sounds. This latter result apparently is due to connections of Ep with the reticular formation, and "arousal" reactions involve Ep as well as other cortical areas (16). As opposed to the response figures, the spontaneous ones have a wider range of variability; their histories are expressible in terms of statistical statements (16).

In the unanesthetized monkey cortex, complex figures can be seen, for example, in areas classically called "sensori-

motor" in the pre- and postcentral gyri--evoked figures after acoustic stimuli, spontaneous ones during sleep, and "sensori-motor" ones during voluntary motor activity (12).

The evoked figures (Fig. 9) are stereotyped for any given state of the animal but vary with the state and with the time after the stimulus. A wide-awake, excited animal has very small, rapid evoked figures, but as it dozes off, the figures become larger, slower, and travel in different apparent paths over the cortex. For example, they start in motor "leg" and go to "arm" when the monkey is lightly dozing; but when it is deeply asleep, they start in "arm" and go to "leg." The early parts of the evoked figures are tied to the stimulus, but the later parts have more variability and finally seem to merge with the "spontaneous" activity. It seems as if the short-latency figures are giving data tied to the stimulus and the state, and the later ones to related data from other regions which may involve habituation and learning. Before we can effectively speculate on these matters, we need more data over wider areas, such as has been done for the motor map found above.

Spontaneous figures during sleep (Fig. 10) travel in such a characteristic fashion that with a little practice one can see, for example, the boundaries between the "arm" and the "leg" regions quite easily. As the animal's state varies from an excited one to deep sleep, the variability of the boundaries decreases.

During voluntary movements, characteristic figures can be seen in the cortical areas from which similar movements are elicitable by electric stimuli, and yet no such figures are seen in the surrounding areas. For example, if the arm strikes, figures show in "arm" area but not in "leg" or "face" (Fig. 11).

Thus, these figures are sensitive indicators of the states and of the activities of the monkey. It is to be expected that as wider areas of the CNS are covered, we shall begin to find closer ties between these figures and behavior even to the point of seeing progressive changes in some of the figures as the monkey progresses in a learning situation.

One is left, of course, with many facts ultimately to be explained by structural connections, neurophysiological factors, and by extremely careful behavioral records and histories. One of the large difficulties in correlating structure, behavior, and CNS activity is the spatial problem of getting enough electrodes, and small enough electrodes, in there with minimal injury. Still another difficulty is the temporal problem of getting enough samples from each electrode per unit of time, over a long enough time, to begin to see what goes on during conditioning or learning, especially when a monkey can learn with one exposure to a situation, as we see repeatedly. As for the problem of the investigator's absorbing the data--if he has adequate recording techniques, he has a lot of time to work on a very short recorded part of a given monkey's life.

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