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OPERANT CONDITIONING OF THE BOTTLENOSE DOLPHIN WITH ELECTRICAL STIMULATION OF THE BRAIN[1]

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The stimulation of motivational systems within the brain has been investigated for small-brained mammals (Lilly, 1958b). The present report is on the investigation of the large brain of *Tursiops truncatus*, the bottlenose dolphin of the Eastern United States.

The bottlenose dolphin was chosen for these experiments to extend the comparative series of animals from those with brain weights smaller than those of man to brain weights equal to and greater than those of man. The basic question is: Are these electrical stimulations of the subcortical motivationally active systems as demanding in the large-brained mammals as they are in the smaller-brained mammals (Lilly, 1958c, 1961)? A series of careful brain-weight measurements were made in relation to the size of the animals (Kruger, 1959). The results of these measurements are plotted in Figure 1. The weights are in the ranges 1,100 to 1,700 gm. The adult human brain weights, as given by Vierordt (1890), are in the lower portion of this range. Earlier investigations on brain stimulation in these systems were on the monkey, *Macaca mulatta* (80 to 105 gm.) (Lilly, 1958b).

The present account is concerned with showing some results of stimulation, emphasizing those which differ from those for the monkey.

METHOD

The dolphins in this study were restrained in a small laboratory tank and suspended in a sling in water in intraspecies isolation. The rostrum was restrained by its insertion into a hole in a piece of plywood lined with polyurethane foam. The neck was held downward by a foam-covered restraint bar. The dorsal aspect of the skin was kept moist with continuously flowing sea water. The exposed portions of the head were kept moist with sea water sprays. The rostral restraint allowed the animal to move the rostrum up and down a distance of 2 in. and laterally a distance of about 1½ in. The flippers and flukes were hanging free in the tank of water.

Previous experiments had shown that general anesthesia (Nembutal or paraldehyde) stops respiration in this species (Lilly, 1958c, 1961). Because of the susceptibility of this animal to respiratory failure under anesthesia, a method was devised to place electrodes within the brain of this animal using only a local anesthetic (Lilly, 1958a). Figure 2 shows the principles of this method in diagrammatic form. In brief, a small piece of hypodermic-needle tubing (sleeve guide) is hammered through the skin, the blubber, the muscle, and is lodged in the skull. A mandrel which carries the sleeve guide during the hammering process can be withdrawn once the guide penetrates the inner table of the skull, as in Phase 3, Figure 2. Up to Phase 3 the tip of the mandrel is held by the bone and one is unable to withdraw it. The protruding tip of the mandrel is freed in the cranial cavity at the instant that the sleeve guide penetrates the inner table. The site is prepared by injection of 1% procaine before the hammering process takes place. With a few blows of a common carpenter's hammer on the upper end of the mandrel, the operation is completed. On the withdrawal of the mandrel, the skin and blubber close, leaving the proximal end of the sleeve guide covered. In the case of the dolphin, a small mark remains in the skin. Later, using this as a guide, one can find the track through the skin, blubber, and muscle and probe for the tip of the sleeve guide at any time that one wishes to insert an electrode pair.

Special electrodes are constructed which fit closely into the sleeve guide. An electrode driver grips the outer end of the sleeve guide which protrudes out of the skull. An electrode pair can be lowered 1 mm. at a time through the guide into the brain substance by this technique. The track is mapped millimeter by millimeter. At the end of a day, electrode and driver are removed and the animal returned to the residence tank free of any wires or connections. The experiment is continued the following day, returning to the same place in the brain with the electrodes. The sleeve guides placed in the dolphin's skull are No. 15 stainless-steel (#316) hypodermic-needle tubing; the shielding grounding the outer conductor of the electrode pair is No. 18 stainless-steel tubing. The inner electrode of the electrode pair is insulated from the outer electrode by a tube of Teflon, and consists of a piece of No. 30 hypodermic-needle tubing which extends beyond the tip of the No. 18 tubing 1 mm. This exposed tip and nearby return electrode give a localization of the stimulus at threshold over a volume which has a radius of approximately 1 to 2 mm. within the brain. The diameter of the outer tubing is 1 mm. Such an electrode is stiff enough to give a straight track through this large brain. A dorsal-ventral track can be up to 120 mm. in length, and a side-to-side track can be up to 200 mm. long. With the use of the proper
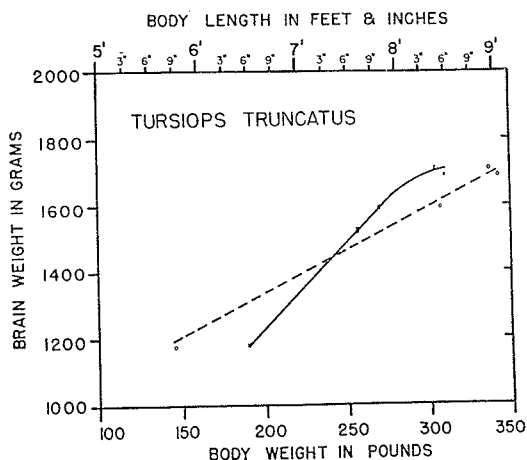
FIG. 1. Brain weight, body length, and body weight for the bottlenose dolphin (*Tursiops truncatus*). (The solid curve is brain weight versus body length; the broken line curve is brain weight versus body weight. Recently, a baby dolphin 5 ft. 4 in. long, weighing 100 lb., was found to have a brain weight of 1,100 gm.)

electrical wave form (Lilly, 1960; Lilly, Hughes, Alvord, & Galkin, 1955) observations can be continued for many hours per day for several weeks. Reproducible results are obtained testing a track during withdrawal of the electrodes, on reinsertions to the same depth at later dates, and during continuous observations at the same site.

A minimum-effort switch (Lilly, 1942) is placed above the salt water and out of the spray. A movable rod is placed near the rostrum of the animal, which usually pushes at once and explores its degree of freedom. The rod is usually adjusted to move in a vertical direction when touched and return to the initial position on release. The *S* quickly determines that this is the proper way to push the rod. As soon as an active spot (Lilly, 1958b) is found, the *S* is permitted to push the rod in order either to (a) turn the stimulus on or (b) turn the stimulus off, depending on the site of the electrode in its brain.

RESULTS

With a naive, untrained *S* of a previously uninvestigated species, the first experiences stimulating either the "rewarding" or the "punishing" systems tax the ingenuity of the investigator. In the case of monkeys we noted that stimulation of a rewarding or self-starting system and a punishing or self-stop system at threshold for the animal to turn on or to shut off the stimulus apparently can be a very mild experience (Lilly, 1958b). In general, little or no vocalizations are emitted at these thresholds in the monkey.

Stimulation of either of these systems in a dolphin leads to vocalization; in the case of the rewarding or self-starting systems the vocaliza-
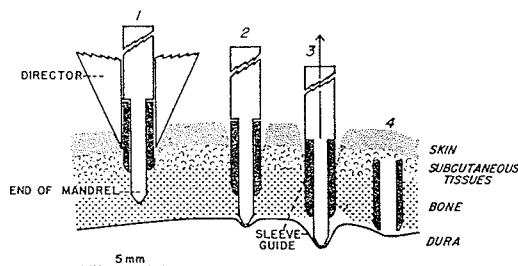

FIG. 2. Stages of penetration of sleeve-guide into bone. (The sleeve is hammered into the bone by hitting the upper end of the mandrel. The director keeps the sleeve and mandrel lined up in the desired direction. At the instant of penetration of the sleeve through the inner table—Phase 3—the mandrel is freed up from the bone, and is easily withdrawn.)

tions are extremely complex and cover the whole known range of whistles, clicks, squawks, and other complex noises (Lilly, 1958c, 1961; Lilly & Miller, 1961a, 1961b) in a few minutes.

In the case of the punishment or the self-stop system, the first experience with a naive animal gives the emission of distress whistles (Lilly, 1958c, 1961)

Self-Start or Rewarding Systems

Illustrations of the kinds of results obtained are given in Figures 3, 4, and 5. With the electrodes in a zone near the head of the caudate nucleus, a dolphin can be quickly induced to turn on the switch to start a train of stimuli of 0.5- to 1.0-sec. duration repeatedly. Figure 3 shows the first such contacts of a naive dolphin.

When the *S* pushes upward on the rod and makes contact with the radio-frequency switch, the trace on this record goes downward. When the animal releases the rod, the trace then returns to the baseline in an upward direction. If *S* maintains contact with the rod, the trace will stay in the downward position. The release of the rod triggers the stimulus. As Figure 3 shows, during the first 12 sec. of the record the *S* pushed once in a very incisive fashion, in a hesitant fashion the second time, and the third time released it quickly. Immediately he touched it again, released it again, and during the next 4 sec. touched and released once per second. The *S* started a train about once or twice every 4 sec. for the rest of the record, except for brief bursts of about one per sec., three-quarters of the way through the record.

This kind of immediately successful behavior of a naive animal we did not find in the
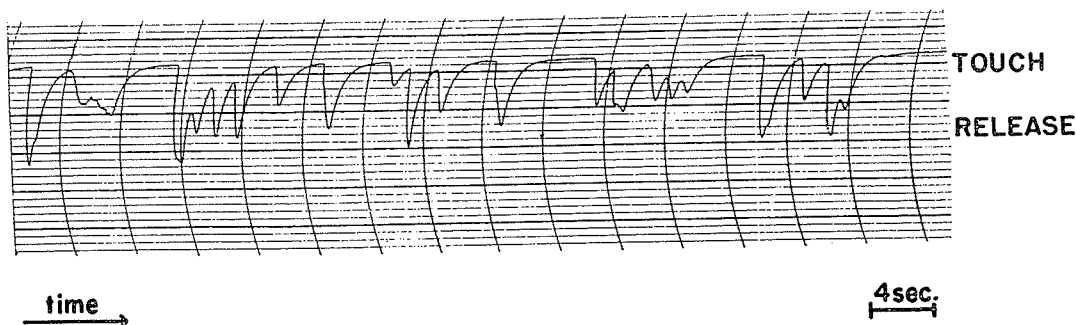
FIG. 3. "Start-capture" record of a naive bottlenose dolphin. (Every time the animal touches and pushes upward on a lever, the trace moves downward and stays down until the animal releases it. Each touch of the lever is symbolized by a small peak in the downward direction. The electrode pair is situated at a depth of 95 mm. below the surface of the rostral dorsal cortex in subcortical white matter near the head of the caudate nucleus. The pulse pair repetition frequency was 60 per second at a positive peak current of 6.0 ma. with a train duration of 1.0 sec. Every 10 sec., the animal was given a free train by the apparatus. This is the *S*'s first set of touches and releases in order to stimulate its own subcortex. Dolphin 7, 1957.)
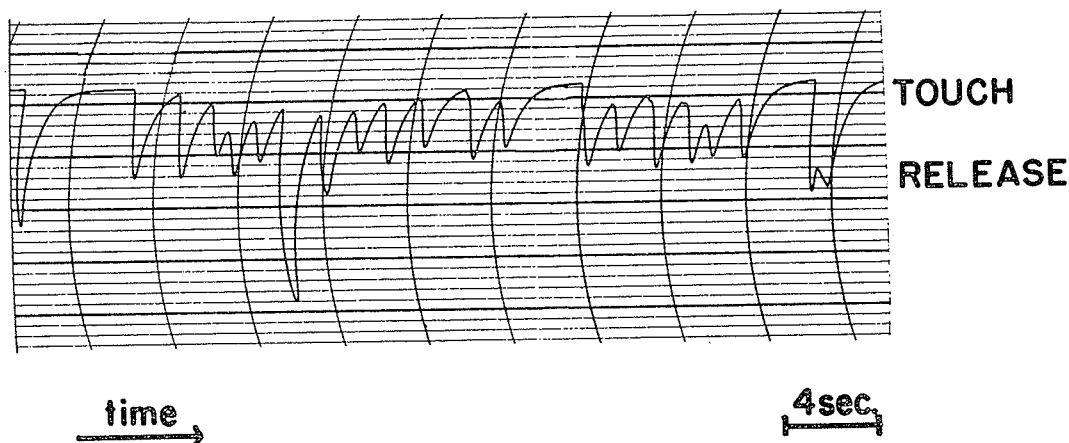

FIG. 4. A later "start-capture" record. (The animal has developed a regular rhythm of pressing the lever: for the train duration of 1.0 sec. the animal pressed at a rate of about 1 every 2 sec.; and for a shorter train duration —0.1 sec.—*S* pushed at a peak rate of 3 per sec. Cf. Figure 3, parameters and loci the same. Dolphin 7.)

case of the monkey. Many random contacts with the radio-frequency switch were necessary before the monkey made the association between touching the switch and the onset of the stimulus. In the case of the dolphins, the cause and effect relation between pushing on the rod and the elicitation of the effect in its brain was made after the first two to three experiences. From this point on this animal continued to push on the rod for many minutes.

A segment of a later portion of the *S*'s record is shown in Figure 4. This record is quite comparable with that of some monkeys using 0.5- and 1.0-sec. trains (Lilly, 1958b).

A monkey can average three times per second with the minimum-effort switch with 0.1-sec. trains. The dolphin with 0.1-sec. trains can reach these rates also. The dolphin is working

under water, the monkey in air. This animal achieved rates of pressing (not shown on these records) up to three pushes per second.

If during this long sequence of self-starting of the brain stimulus the current is interrupted, either by accident or by design, and not allowed to enter the brain of the animal, the *S* immediately starts a series of vocalizations. These sounds resemble those produced by the naive animal when first stimulated in these systems. During the previous sessions of pressing the switch to receive the electrical stimulus, the *S* worked silently without any vocalization.

Figure 5 shows such a vocal effect in a graphic form. At the left of the figure the current has just been interrupted. This record is the rectified integrated output of an amplifier

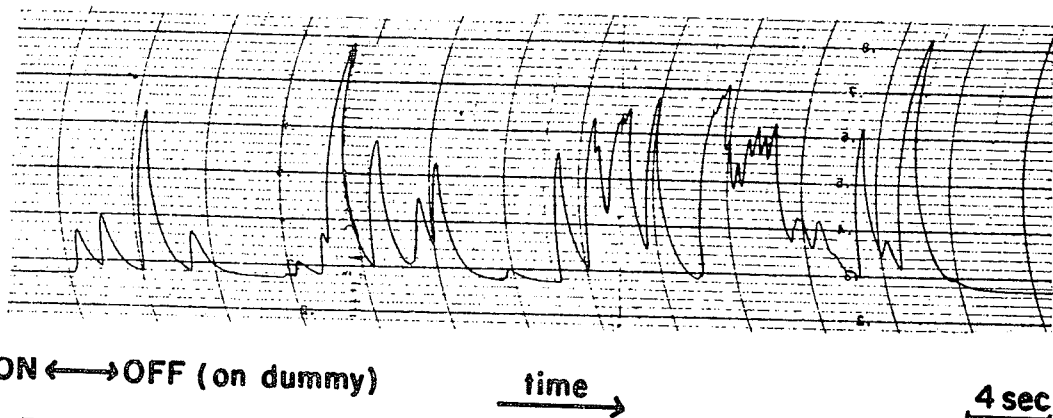ON ←——→OFF (on dummy)   time →   4 sec.

FIG. 5. Vocalization after an interval of "start-capture" activity. (An upward deflection in this record means vocal activity of some sort. The pen is deflected by the integral of the rectified electrical acoustic output. The louder and the more prolonged the noise, the farther the pen is deflected in a given short period of time. This record starts immediately after the current is removed from the stimulating electrodes by turning off the switch to the animal—"on dummy"—so that S no longer can stimulate itself. Within a few seconds of that time, the S starts to vocalize, in this case continuing its vocalization for an interval of 40 sec. Parameters are as in Figures 3 and 4. Previous to the time of this figure, the S had been nonvocal while stimulating its own brain by pressing the lever at a rate of about one per sec. Dolphin 7.)

fed by an air microphone suspended near the blowhole. The series of air-borne sounds emitted here consisted of whistles, bronx-cheer-like noises, squawks, blats, very rapid and loud clickings and other extremely complex vocalizations (Lilly & Miller, 1961a, 1961b), the result of the withdrawal of a "rewarding" (positively reinforcing) experience in a trained animal.

Another animal (Dolphin 8, 1958) stimulated in a similar region was induced to vocalize in a particular way in order to obtain the brain stimulation. From its vocalizations a whistle, in air, of a particular frequency, duration, and amplitude was chosen as the sufficient condition for giving a brain stimulus.

It was found that the S quickly learned some of the rules of this game. The S emitted whistles of varying characteristics from one whistle to the next. The proper whistle was quickly shaped up. Every time the S whistled a particular pitch, it was "rewarded"; within a period of 10 min. S was whistling this particular duration, pitch, and amplitude. As in the case of the monkey, it attempted to reduce the effort put out in order to obtain the reward: it tried to lower the amplitude, keeping the pitch and duration constant; by the withholding of. reward, it could be induced to whistle loudly again.

A similar series of experiments with rhesus monkeys in similar systems within the brain

showed that one can increase the *total amount* of daily vocalization, but one cannot induce the monkey to *use* vocalization the way it uses its hands in order to start a desired stimulus. The dolphin apparently uses vocal outputs and may even prefer vocalization to pushing a lever with its beak. As in the case of the human, there is less "central effort" for vocalization than there is for the monkey and for the action of the larger muscles of the body (Lilly, 1958b; Lilly & Miller, 1961a, 1961b).

Stop Systems

As was stated above in the case of the naive animal, we have found that dolphins tend to emit a more stereotyped series of vocalizations when we stimulate a negative, or "punishing," or "stop" system zone. The monkey can easily be trained to shut off a stimulus at a critical threshold, and the threshold for such phenomena is determined by means of a crescendo train of stimuli (Lilly, 1958b). The train of stimuli starts near zero, builds up linearly with respect to time, i.e., the pulses increase in intensity over a period of time, are automatically shut off by the apparatus, and after a pause are started once again. At any time the S can shut off the current. A typical result is shown in Figure 6.

The S is given a switch which shuts off the stimulus the instant that S releases its contact. This task a monkey learns relatively rapidly

after rather few trials. If the peak of the crescendo is carried high enough to cause violent "escape" behavior, a trained monkey will shut off the stimulus at a threshold most of the time well below that where one can detect any clinical signs of increased autonomic activity or "escape" behavior (Lilly, 1958b). As was reported previously, the threshold for detection by the monkey of stimulation in such a system is about one-third to one-fifth the threshold for its imperative shutting-off of the stimulus. At currents only a few percentage points above the imperative value, the monkey is no longer able to shut off the stimulus. A physiological state of violent escape activity takes over all the paths to motility.

Similar results have been found with the dolphin. The only dramatic differences are the speed with which the naive dolphin learns the task and its developed control of the escape pattern. Within the order of 3 to 20 trials, the dolphin is pushing regularly at the value it will be pushing several hours later. If one shuts off the current, the dolphin immediately stops pushing the lever. The monkey may push it two or three times beyond the instant at which the current is shut off by the operator. Figure

6 illustrates the threshold level at which the S pushes the lever to shut off the current and the immediate cessation of pushing when the current is turned off. It is to be noted that in this figure there is no particular time relationship between the respirations of this S and the pushing of the switch. The head movements of respiration did not interfere with the head movements necessary for moving the rod.

As in the case of the rewarding systems, the S did not vocalize during this period while pushing the switch in order to shut off the current. In contrast with the stimulation of "rewarding" systems there was no vocalization when the current was cut off from the S. One could obtain vocalization, that is the distress call, at a threshold somewhat above that at which the S was pushing the switch in order to shut off the current.

Figure 7 shows a quantitative plot of the analysis of 588 successive crescendo exposures. The total number of times that the S shut off the current was 564 in 588 trials, i.e., its over-
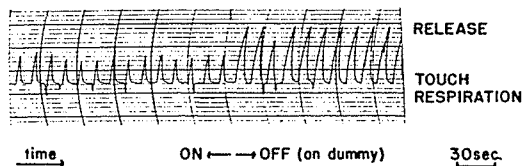

FIG. 6. "Stop-capture" record after a short period of learning. (Respiration is shown by a slight downward deflection of the pen. Increasing stimulus intensity is shown by an upward deflection of the pen occurring regularly every 13 sec. After the fourteenth upward deflection, the current was shut off, i.e., the S was not allowed to receive any further stimulation in this portion of its brain. The left half of the record shows the accuracy with which the S was choosing the value of current at which it would push the shutoff switch. No errors on the part of the animal are shown on this record. The right half shows the peak current to which the apparatus would carry the current if the S had not shut it off. There is no regular relationship between the respiration and the pushing of the lever. The electrodes are located in the thalamus at a depth of 60 mm. below the dorsal cortical surface. The electrical stimulus is occurring at a rate of 60 pulse pairs per sec. in crescendos starting at a current of approximately 0.3 ma. and rising to a peak of 2.9 ma. unless shut off earlier by the animal. The crescendo repetition rate is one every 13 sec. controlled by the apparatus. Dolphin 6—1957. Detailed analysis of such records is shown in Figure 7.)
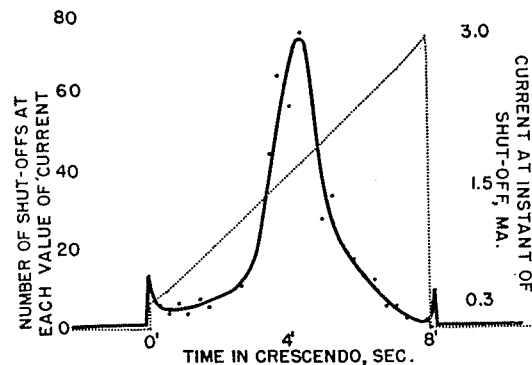

FIG. 7. Analysis of the distribution of thresholds for "self-stop" activity. (The dotted curve is the course of the crescendo of current with respect to time if the animal does not shut off the current. The solid curve is the distribution of frequencies of occurrence of the shutoffs at each value of current for the exposure to a total of 588 crescendos. Of these total exposures, the animal shut off 564. The baseline gives the time in seconds after the beginning of the crescendo. The ordinate for the solid curve is the number of shutoffs at each value of current; for the dotted curve, the current at the instant of shutoff in milliamperes. The peak of the solid curve occurs at approximately 4.1 sec. after the beginning of the crescendo, i.e., at a current of 1.7 ma. Beyond this peak, as in the case of the macaque, the animal becomes too emotionally upset to push the lever. The parameters of the electrical stimulus are 60 pulse pairs per sec., from 0.3 to 2.9 ma., lasting 8 sec. and repeated once every 13 sec. Dolphin 6.)
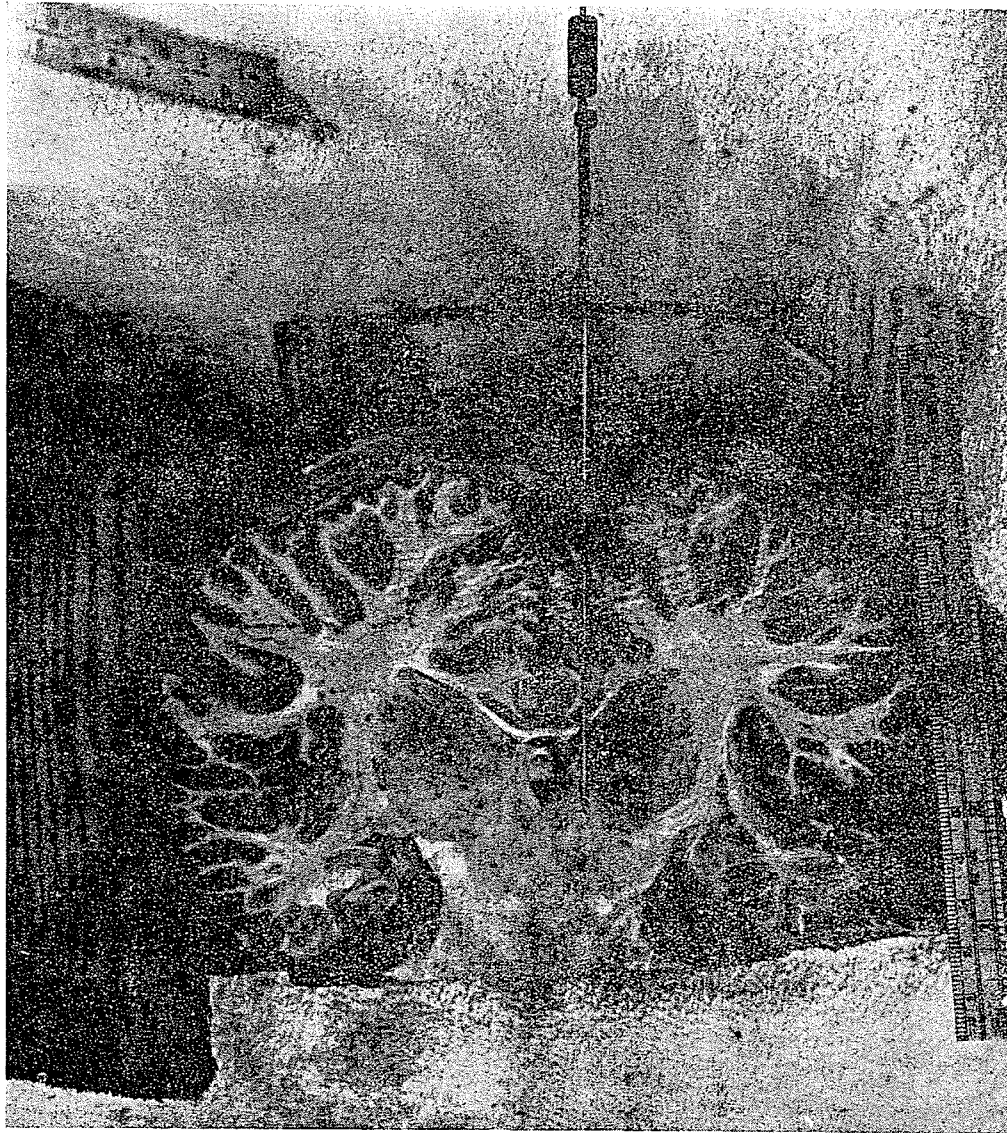
FIG. 8. Location of the electrodes in the thalamus. (This cross section illustrates the size of the dolphin's brain and shows the locus of the stimulations for Figures 6 and 7. The track down to this point was explored, and is seen filled with the No. 18 hypodermic-needle tubing of the outer, grounded electrode. Some motor responses including respiratory ones were found above this negative zone. Dolphin 6.)

all score of 95.9% was comparable to that of a well-trained monkey. A detailed analysis of the currents for each of these shutoffs gives the statistical distribution shown in this figure. As in the case of the monkey, there is a small "detection" peak at the beginning of the step (0.3 ma.) of the crescendo. Most of the imperative shutoffs occur at a threshold of slightly over 1.7 ma. with these particular parameters.

As in the case of the monkey, this imperative peak precedes (in terms of rising current) the appearance of clinical signs. In the case of the dolphin, the first clinical sign is vocalization, the distress call. This call is elicited only by trains not under the control of the dolphin which are of a current larger than 1.6 ma. After the first few exposures, violent escape behavior is not elicited at any of the currents to which we exposed these Ss: the most activity elicitable is briefly shutting both eyes tightly (as these Ss do in painful needle pricks), sharp withdrawals, jumps of the head and body, or

their "warning negation"—vertical or horizontal rapid head-shaking. This apparent control is contrasted with the violent pushing, pulling, running, and biting of the *macaque* similarly stimulated. However, after a long period of confinement with humans, a dolphin begins to act more violently. A naive dolphin in restraint tends to inhibit the violence for unknown reasons. Over months it tends to become less inhibited toward humans and its restraints. If we remember that a 3C0- to 400-lb. dolphin has great muscular power and could destroy, or at least badly damage, itself, the restraint systems, and possibly even the investigator, it is very surprising to find that dolphins are not more violent under such "punishing" stimulations as these. Their behavior resembles that of a very strong-minded human being who, during bouts of intense pain, can sometimes attenuate his desperate behavior more than can the "lower" animals.

The particular spot in the brain stimulated for the previous two figures is shown in Figure 8. It is about 8 mm. lateral to the mid-plane in the *S*'s thalamus. Presumably this is a portion of the system which in the human causes the thalamic pain syndrome when stimulated (Monnier, 1955). Other such spots have been studied also.

SUMMARY AND CONCLUSIONS

It is shown that it is feasible to place electrodes into the large brain of the unanesthetized bottlenose dolphin (*Tursiops truncatus*). Using roving electrodes, one can demonstrate separate zones of the brain which are positively and negatively reinforcing, i.e., in which "self-start" and "self-stop" activity can be elicited. It is shown that the dolphin learns these tasks more rapidly than does the monkey. It is also shown that in a rewarding, or positively reinforcing zone, the animal tends to vocalize in complex and startling ways. It vocalizes when first stimulated in this area or when stimulation is withdrawn after a period of "self-start" activity.

Thus we conclude that the behavior of the bottlenose dolphin differs from that of the monkey in the following respects: Like the monkey, the dolphin uses any available external somatic motor output in order to push switches to stimulate its own brain for a wanted, or positive, or rewarding stimulus or to cut off an unwanted, or negative, or punishing stimulation started by the apparatus. In contrast with the monkey, the dolphin uses its vocal output when this is effective in order to modify the responses obtained from the environment (in terms of brain stimulation). The dolphin can inhibit violent escape behavior caused by "punishing" brain stimulation; the *macaque* does not. The large brain of the dolphin thus affords: (*a*) faster learning, (*b*) greater control over reactions to stimulation of subcortical systems which are motivationally active, and (*c*) control and use of vocalizations to obtain "rewards" and to stop "punishments."

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