REINFORCING PROPERTIES OF AROUSAL

by

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It has recently been shown that rodents and primates will
work to achieve changes in the level or pattern of sensory stimulation
in their environments. For example, it has been found that mice (Kish,
1955), rats (Marx, Henderson and Roberts, 1955), and monkeys (Moon and
Lodahl, 1956) will increase their bar-pressing rates in a Skinner-box
if depression of the bar produces an increase in the level of illumination.

Most workers in the field, however, seem to view these studies
as but one aspect of a larger group of experiments demonstrating the re-
warding properties of certain changes in sensory stimulation. Thus,
Harlow (1953) has argued for the underlying similarity of the motivation
involved in bar pressing for light and that involved in a wide variety
of other experiments including the learning of a maze by rats for the
privilege of exploring a new maze, the solution by monkeys of mechanical
puzzles for the intrinsic intellectual activity, or the operation by
monkeys of a mechanical latch for the reward of looking out into the
laboratory through a small window. The "exteroceptively aroused drives"
with which Harlow attempts to relate these studies is apparently intend-
ed to encompass the same range of behaviors as "the will to perceive"
previously noted by Woodworth (1947) or Pavlov's "investigatory reflex"
(1941). Other psychologists (Hebb, 1955 b; Dember and Earl, 1957) have
also grappled with the problem of eliciting a unifying principal which
could be used as a guide in grouping an agreed upon body of data. Hebb
(1955 b), for example, has suggested that, "The curiosity drive .....
might be considered to cover both investigatory and manipulatory activities
on the one hand, and exploratory, on the other. It would also comprehend

the "problem-seeking" behavior recently studied by Mahut and Havelka at McGill." He further noted that, "... a sort of exploratory-curiosity-manipulatory drive, ... essentially comes down to a tendency to seek varied stimulation."

The search for a unifying mechanism was soon carried to the physiological level. Fortunately, the previous decade's work on the reticular activating system (RAS) had disclosed a functionally defined anatomical system where impulses from all sensory modalities converged. Moreover, stimulation of this system was shown to have an arousing effect both on the electrocorticogram and behavior. Thus, psychologists casting about for some means of relating the diverse behavioral observations of reward produced by sensory change were provided with a promising physiological substrate -- the ascending reticular formation. The possible relationship between the rewarding effects of sensory stimulation and the RAS was accordingly noted by Sharpless (1954) and Hebb and Mahut (1955).

To apply this line of speculation in a concrete situation, one might consider the rat bar-pressing for light reward in a Skinner-box. The hypothesis put forth by the aforementioned workers suggests that the reinforcing effects of light are mediated, in part at least, by activity induced in the activating system of the brainstem. If reinforcing effects could be shown to result from direct stimulation of the activating system, it would provide some preliminary support for the postulated linkage between the rewarding effects of sensory change and the arousal system. The self-stimulation technique developed by Olds and Milner (1954) offered a possible means for the direct investi-

gation of this implication. In the study to be described in the present

paper, rats were run through a Skinner-box procedure similar to that used

by investigators examining the rewarding properties of light or sound,

except that a pulse to the brainstem reticular formation was substituted

for the flash of light or click.

BEHAVIOUR REINFORCED BY SENSORY CHANGE

In formal terms, the literature to be surveyed in this section involves a class of behaviour defined partly by inclusion and partly by exclusion. That is, we shall be concerned with behaviour reinforced by changes in sensory stimulation with the exception of those cases where this change is, or has been, associated with the commonly accepted drives requisite to the survival of the species, such as hunger, thirst or sex. This includes a wide range of experiments dealing with exploratory behaviour, the response to novelty, investigatory reflexes and the like. The class of behaviour under discussion has been most commonly catalogued under the heading of "curiosity". We shall now turn to a survey of its place in the history of psychology.

No references to curiosity or novelty-seeking behaviour are to be found in either Murchison's (1934) or Stevens' (1951) comprehensive handbooks covering the field of experimental psychology, although comments on the subject are to be found in the somewhat earlier text of Murray (1885). Murray, who was at the time Professor of Philosophy and Psychology at McGill University, anticipated one of his successors by some 70 years (Hebb, 1955 b) with the observation that, "Curiosity.... an intellectual emotion....when not overstrained, is itself an agreeable activity" (Murray, 1885, p.386).

At the time Dr. Murray wrote, however, curiosity was still thought to be largely confined to man. Interest in the possibility that animals might possess so advanced a motive as curiosity came about as a

direct result of the rise of evolutionary doctrine in the latter half of
the 19th century.   Before that time it was tacitly assumed that human
and animal motivation differed qualitatively as well as quantitatively.
This was expressed in straightforward fashion by Leroy, a French ranger
of the 18th century.   In a series of letters, published in English after
his death, Leroy noted that:

   "Now animals, clothed by nature, are only excited to attention
   by the wants of appetite and love.   They are without these
   conventional wants which are the fruit of leisure and ennui.
   The need of excitement presses upon us in the waking state, and
   produces the uneasy curiosity which is the parent of knowledge.
   Animals are without this want" (Leroy, 1870, p.127).

        Some individuals attempted to narrow the ground still further
by restricting the higher "appetites" to a select few even among human
beings.   Thus, the aforementioned Professor Murray showed the true psycho-
logist's suspicion of his fellow man by noting that, "In later life, it is
only among men of some education that it (curiosity) forms a useful and
refining power" (Murray, 1885, p.386).

        There was, however, one group which was vigorously opposed to
views limiting motives such as curiosity to one particular species.   This
group was composed of men identified to varying degrees with the evolution-
ary movement, from Darwin himself to George Romanes and Lloyd Morgan.
In "The Descent of Man", Darwin (1874) at one point explicitly set out to
"....show that there is no fundamental difference between man and the
higher mammals in their mental faculties."   Specifically in regard to

curiosity, Darwin noted that "Animals manifestly enjoy excitement, and suffer from ennui, as may be seen with dogs, and according to Rengger, with monkeys.   All animals feel Wonder, and many exhibit Curiosity."   Even within the evolutionist movement, however, there was opposition to the continuity-through-man point of view coming from so distinguished a source as Alfred Russell Wallace (1871, Chap10; 1911, p.374).   Darwin's and Romanes' myriad observations on animal behaviour generally, and curiosity behaviour in particular, can best be understood as an attempt to demonstrate the continuity of mental processes in the face of opposition from both inside and outside the evolutionary movement.

The earliest empirical study of curiosity behaviour which the writer has found was carried out at an English Zoo about 1870.   In view of the astuteness of the observations, and its historical importance, it is probably best to reproduce the incident as it was originally described:

"Brehm gives a curious account of the instinctive dread which his monkeys exhibited toward snakes, but their curiosity was so great that they could not desist from occasionally satiating their horror in the most human fashion -- by lifting up the lid of the box in which the snakes were kept.   I was so much surprised at his account that I took a stuffed and coiled up snake into the monkey house at the Zoological Gardens, and the excitement thus caused was one of the most curious spectacles which I ever beheld... I then placed the stuffed specimen on the ground in one of the larger compartments.   After a time all the monkeys collected round it in a circle, and, staring intently, presented a most ludicrous appearance....I then placed a live snake in a paper bag, with the mouth loosely closed, in one of the larger compartments.   I then witnessed what Brehm has described, for monkey after monkey, with head raised high and turned on one side, could not resist taking momentary peeps into the upright bag at the dreadful object lying quiet at the bottom."

The investigator in this case was no less eminent a
scientist than Charles Darwin (1874) and, while he was undoubtedly en-
couraged by the human fashion with which the monkeys sated their curiosity,
it is not difficult to understand his surprise at their highly unadaptive
behaviour.   Peeping at snakes would not seem to be a pastime conducive to
the survival of even the most robust species of monkey.   Moreover, these
observations of Darwin, were later confirmed independently by the American
psychologist Kinnaman (1902).   Thus, there existed a very real problem for
the evolutionists in relation to curiosity behaviour, the crux of which was
the peculiar ability of certain objects to excite both fear (avoidance) and
curiosity (approach) behaviour.   Numerous observations along these lines
were made by other early workers in the field.   Romanes (1884) describes
in some detail the unusual conflict behaviour of his pet dog when confronted
by a soap bubble, while Groos (1898) noted that, "The curiosity of a dog is
very ludicrous when a beetle runs before him;   evidently he is a little
afraid of the tiny creature, but he cannot resist until he has smelled it
all over".   It fell to William James (1890), however, to finally resolve
the problem in typical pragmatic fashion.   First, he noted that early in
the vertebrate series, curiosity might be evoked by any novel object and
further that curiosity and fear are, "...antagonistic emotions liable to
be awakened by the same outward thing."   James was then able to settle all
difficulties as follows: "Inasmuch as new objects may always be advantageous,
it is better that an animal should not absolutely fear them.   But, inasmuch
as they may also possibly be harmful, it is better that he should not
quite be indifferent to them either...."

The observations of men like Darwin, Romanes and Groos,
on the conflict between fear and curiosity, have since been confirmed
in the experimental laboratory (Montgomery and Monkman, 1955; Montgomery,
1955). Moreover, McDougall (1911), Woodworth (1921), Hebb (1955 b) and
other psychologists writing since James, have observed and discussed the
antagonistic relationship between fear and curiosity. It should be kept
in mind, however, that the basic observations relevant to this problem were
well established at the beginning of the 20th century. This situation
prevailed not only in regard to the fear-curiosity relationship, but also
in respect to the basic observations on manipulatory and visual exploratory
activities of monkeys, dogs, and other animals.

Romanes' sister in 1881 had made extensive observations on a
pet monkey who would screw and unscrew the handle of a brush, or repeatedly
open and close a trunk lock which he had learned to operate, with no apparent
reward other than the satisfaction inherent in the manipulatory activity
(cited in Romanes, 1883, pp.490-492). Thorndike (1901) describes a monkey
who would similarly sit in his cage for long periods pulling on a taut wire,
presumably for the reward of listening to the resultant "twang". As Dennis
(1955) has pointed out, these observations antedated the next such obser-
vations in the English speaking world by approximately 50 years.

In fact, the attracting, or what modern psychologists would call
the reinforcing properties of novel sensory stimuli were widely recognized
by many individuals of earlier times who had occasion to work with animals.
Tennant (cited in Groos, 1898) has described a novel method of hunting used in

Ceylon which consisted in tying lights to the backs of tame buffalo, fastening bells around their necks and setting the animals loose at night. It is reported that all sorts of wild animals, "attracted by curiosity", came to look at them and thus were captured. An analogous technique is said by Lloyd Morgan (1891) to have been used in capturing a particular variety of deer on this continent.

Many examples of this sort could be given. The literature is rife with descriptions of dogs (Groos, 1898) and monkeys (Kinnaman, 1902) staring out of windows for the pleasure of observing the goings-on outside; and even includes a fanciful description of a group of cows that formed an appreciative, albeit not too critical, audience for a solitary landscape artist -- who supposed the animals to be motivated by a visual aesthetic instinct.

As may be gathered from the last example, the early observers had not yet been indoctrinated with Lloyd Morgan's canon and were often more enthusiastic than accurate. This should not obscure the fact, however, that they did manage to uncover a great many of the basic facts of behaviour reinforced by sensory change. Nor should the occurrence, in the early literature, of statements that goats and nightingales were among the most curious of all animals (Sheitlin, cited in Groos, 1898) blind us to the astuteness of many of the contributions.

Nearly every eminent comparative psychologist from Darwin, through Romanes, Morgan and Thorndike, had made notations of varying length

describing certain aspects of curiosity behaviour in animals.
Nevertheless, with the rise of experimental animal psychology,
laboratory experimentation on the phenomena of curiosity dwindled to
near zero, and was to remain almost quiescent for at least 25 years.
The reasons for this decline are probably to be found in the preoccupation
with learning during the first half century of laboratory experiment in
animal psychology.   In conducting learning experiments, curiosity, and
the resultant exploratory behaviour were regarded as more hinderance than
help and evidence of this attitude often filtered into the psychological
literature of the early 20th century.   Moreover, with such readily manipul-
able motivational variables as hunger, thirst, or electric shock, there
seemed to be little point in dabbling with so tenuous and seemingly un-
predictable a motivation as curiosity.   The following excerpts from an
article by Hicks (1911) appear to represent the general feelings about the
role of curiosity in maze learning:

> "Timidity and curiosity are natural tendencies of a rat in new
> surroundings, and these tendencies must be overcome or inhibited,
> before their trials become automatic.... Curiosity attracts rats
> into blinds and leads them to explore every crook and corner of
> the true path....The curiosity factor...is present long after the
> association has been established, and after errors are eliminated...
> The problem is one of adaptation of an animal with a given nature
> to the maze."

The significance of the last quoted sentence appears to have
been first appreciated by Lashley (1918) who was able to facilitate learning
of a simple maze by allowing the animals a period of pre-test exploration.
In the same paper, Lashley was to report the "spontaneous alternation"

phenomenon which has occupied the attention of many psychologists in recent years. Apart from Lashley's research, however, there was little if any work on curiosity behaviour prior to 1925 and relatively little in the years prior to 1950.

On the literary front things were considerably more active. Freud, McDougall, Woodworth, Pavlov and Tolman had all discussed some aspect of curiosity before 1926, although only the writings of the latter two individuals were to inspire any experimental work directly.

Sigmund Freud's (1905) ideas on the subject certainly occupy a unique position, although to the best knowledge of the writer, they had no impact whatsoever on laboratory research. Freud wrote of "an impulse for knowledge and investigation" which represented a sublimated form of aquisition ~~ory~~ behaviour. This was presumably closely related to the looking impulse (voyeurism) and supposedly derived from the "oral" stage desire to incorporate external objects.

Writing from a somewhat different vantage point, McDougall (1911) also expressed some definite opinions on curiosity behaviour. Proceeding directly to the problem of defining the adequate stimulus for the arousal of curiosity, McDougall wrote: "...the condition of the excitement of the impulse of curiosity seems to be in all cases the presence of a strange or unfamiliar element in whatever is partially familiar." This early insight of McDougall's was somewhat different from the position taken by most other writers of the time. The generally accepted point of view was that novelty

was the prime requisite of the curiosity arousing stimulus, with little regard to the context in which the novel stimulus appeared. It is interesting to note that Berlyne (1950) has incorporated McDougall's ideas in his formulation of the problem of curiosity-motivated behaviour.

In 1921, Woodworth clearly put forth the simple non-contextual view that the stimulus for curiosity is a new or unfamiliar object, familiar ones being taken for granted arouse little exploratory response. He wrote that the child "....approaches what arouses his curiosity and embarks on little expeditions of exploration. Similar behaviour is seen in animals and is without doubt instinctive."

Although curiosity continued to constitute an acceptable textbook topic during the 1920-1950 era, little research was carried out directly on the problem. There were, however, two lines of research initiated in the twenties which form a bridge with current experimentation. The first tack is that initiated independently by Lashley (1918), Tolman (1925) and Dennis and Henneman (1932). The phenomenon in question came to be known as spontaneous alternation. The second body of experimentation which runs from the early twenties to the present has been carried out largely in the Russian laboratories of Pavlov and his successors. Knowledge of this work is limited primarily to bits and pieces published in translations of Pavlov's books and lectures. However, one paper which has fallen into the writer's hands, discussing the curiosity and manipulatory activities of monkeys (Voitonis, 1936), is impressive evidence of the astuteness of the

observations of the Russian workers.

Variability of Response

Using a simple maze with one cul de sac, Lashley (1918) ran 49 rats for food reward. Of these 49 animals, 25 made the correct turn and were rewarded on the first trial. On the subsequent run, however, only eight of the 25 rewarded animals again made the correct turn, the remaining 17 preferring to go to the as yet unexplored side. This result was in opposition to what would normally have been predicted from the law of effect and Lashley concluded that it "seems to indicate an instinctive tendency to varied activity or to a thorough exploration of the environment." Lashley's basic finding was subsequently verified by other investigators (Tolman, 1925; Wingfield and Dennis, 1934).

Two principal explanations have been advanced in an attempt to account for alternation behaviour. The first relies on the positive exploratory tendencies hypothesized by Lashley. The second postulates a "negative" drive, namely the attempt of the animal to avoid repetition of a particular response. Interest in this second explanation was enhanced by Hull's (1943) adaptation of the reactive inhibition postulate, which states the reaction decrement hypothesis in more formal terms.

In retrospect, sufficient data to rule out a simple explanation by response avoidance were available as early as 1934. However, the nail was to be driven into the coffin many times during the next 20 years.

First, Dennis and Sollenberger (1934) observed that, in maze exploration, the sequence of locomotor responses is ordered as to place and not as to response, since there was no tendency to alternate right and left turns. Second, in the above study and in a subsequent experiment by Dennis (1935), the alternation phenomenon was shown to operate in satiated rats using a "pure" exploratory situation without food present in the maze. The problem posed by this study for a drive reduction explanation of alternation behaviour, such as that derived from Hullian framework, would be that of first explaining why the animal runs at all. This, in turn, would require the postulation of an exploratory drive. Finally, Wingfield and Dennis (1934) ran animals in a situation offering four possible routes to food. Forty-three percent of the group chose to run through all four paths, whereas according to chance only, nine percent would vary their responses to this extent. These results were taken by the authors to indicate that there is not just a simple tendency for response alternation, but rather a positive seeking of varied pathways on the part of the rat.

A further series of investigations, carried out by Krech (1937 a, b) also substantiated the belief that rats would actively seek environmental variation. Thus, rats offered a number of paths to a goal box containing food consistently tended to vary their routes. In addition, Krech (1937 a) found that cortical lesions reduced this variety-seeking tendency. In fact, if one considers the shortest route to the goal to be the "true path" and all deviations from this to be errors, it

was possible to arrange a situation where the lesion animals made
significantly fewer errors than the normal rats (Krech, 1937 b).
This variety-seeking behaviour noted by Krech, in hungary rats running
a maze for food reward, appears to be quite similar to the problem-
seeking behaviour observed more recently by Hebb and Mahut (1955) and
Havelka (1956).

The deduction from Hull's (1943) reactive inhibition
construct which elicited the most attention was that increasing effort-
fulness of task should result in an increase in alternation behaviour.
The studies of Mowrer and Jones (1943), Montgomery (1951) and Riley and
Shapiro (1952) indicated, however, that degree of effort played little,
if any, role in alternation behaviour.   Through the use of a cleverly
designed cross-shaped maze, Montgomery (1952) and Glanzer (1953) were
able to oppose "place" and "response" alternation tendencies.   One axis
of the maze constituted the starting boxes and the other the goal boxes.
The animals were alternately started from one end of the "start axis" and
then from the other.   Under these conditions, the animals were consistent-
ly found to enter the least recently occupied goal box, in spite of the
fact that this necessitated making two successive right or left turns.
Montgomery was satisfied to explain this on the basis of exploratory
tendencies.   Glanzer, however, formulated a "stimulus satiation hypothesis"
to account for his findings.   According to this notion, an animal "satiates"
with exposure to a particular stimulus.   Further, as the satiation to a
stimulus increases, the probability of responding to that stimulus decreases.

At this point, there would seem to be no clear-cut way of distinguishing between the apparently different explanations advanced by Montgomery and Glanzer.

The subsequent studies of Walker and his associates have served to dissect out the crucial variables in the Montgomery-Glanzer situation. Thus, it was shown that stimulus (intra-maze cues), place (extra-maze cues), and response variables influence alternation behaviour in descending order. That is "response was found to have little, if any, importance; place had a considerable importance; and the stimulus had more importance than place" (Walker, Dember, Earl and Karoly, 1955). Further, exposure to the stimulus had to occur in context if that exposure was to influence alternation performance reliably (Walker, Dember, Earl, Fliege and Karoly, 1955). Finally, it was demonstrated that a significant amount of response alternation could be produced by properly manipulating the experimental conditions. However, the authors note that "....since it is response quality and not response intensity which influences choice alternation, Hull's concept of reactive inhibition, without considerable modification, is inapplicable to studies of spontaneous alternation" (Walker, Dember, Earl, Fawl and Karoly, 1955).

Alternation behaviour has also been demonstrated in human subjects (Wingfield, 1943; Berlyne, 1951). "Response avoidance" again seems to play a minor role in such behaviour.

Thus the long series of experiments on alternation behaviour

have supported Lashley's original explanation in terms of exploratory
tendencies.   In establishing the independent existence of a curiosity
drive, however, it was necessary to go beyond the above experiments and
demonstrate that curiosity could serve to "energize" learning and per-
formance.   Nissen (1930) had published some highly suggestive, albeit
statistically insignificant, results indicating that rats would cross
an electric grid to explore a Dashiell type maze.   This evidence for
an exploratory drive was supported by Mote and Finger's (1942) finding
that rats would, for a few trials at least, reduce the latency of traversal
of a straight alley even though there was no reward present in the apparatus.

However, the first large scale studies which clearly demon-
strated learning motivated by a curiosity drive were carried out by Harlow
and his co-workers at Wisconsin.   In 1950, they published a series of
reports (Harlow, 1950; Harlow, Harlow, & Meyer, 1950) which indicated that
monkeys would learn to solve simple mechanical puzzles for the intrinsic
reward of manipulation.   In fact, the introduction of food deprivation
seemed to interfere with this learning process.   In subsequent experiments
it was shown that monkeys would also learn a wide variety of discrimination
problems for the privilege of solving mechanical puzzles (Harlow & McClearn,
1954) or getting a brief opportunity to look out into the laboratory
(Butler, 1953).

These experiments were supplemented by a number of studies
with rats.   It was found that rats would learn a maze (Montgomery, 1954)

or discrimination problem (Montgomery & Segall, 1955) if the correct
solution was rewarded by allowing a limited period of exploration of a
complex maze.   Berlyne (1950, 1955) carried out a series of studies
which clearly indicated that rats remembered stimuli to which they had
been exposed before.   Thus, they would spend more time in the vicinity
of a novel object than a familiar one.   This differential response to
stimuli on the basis of prior exposure necessarily implied that learning
had taken place which was presumably reinforced only by reduction of a
curiosity drive.   Thompson and Solomon (1954) have reported the spon-
taneous discrimination of different visual patterns apparently based on
the same principle.   Finally, it has been conclusively demonstrated that
rodents and monkeys will learn an instrumental response, such as bar-
pressing in a Skinner box, if a burst of light accompanies each such
response (Marx et al, 1955; Kish, 1955; Moon & Lodahl, 1956).

Thus, there have appeared in the last few years a large
number of studies which support the view that curiosity can motivate
learning.   At the same time, however, a parallel series of experiments
has been devoted to the investigation of specific variables presumed to
affect curiosity behaviour.   The majority of such studies are concerned
with the relationship between exploration and other drives, namely, activity,
hunger, thirst and fear.   We shall now turn to a consideration of this
literature.   The reader should be warned that it is confused, contra-
dictory and unsystematic.   No simple generalizations emerge in any of these
areas with the exception of the previously discussed antagonistic relationship

between fear and curiosity.

Curiosity Behaviour and Activity Level

Experiments conducted in recent years have strongly supported the notion, previously put forth by Murphy (1947) and Hilgard (1953), that activity is a legitimate independent drive.   Thus, Hill (1956) has shown that restriction of activity will lead to proportional increases in subsequent wheel-turning behaviour, and Kagan & Berkun (1954) have demonstrated that animals will press a bar for the privilege of running in an activity wheel. At least superficially, the activity drive would seem to be within the scope of our review of the non-homeostatic, behaviour-reinforced-by-sensory-change literature.   In this case, the reinforcing sensory impulses would be identified primarily with the proprioceptive feedback from the peripheral musculature.

However, experimenters in the field have been reluctant to place the activity drive in the same class as exploratory, novelty-seeking or investigatory behaviour.   The most often cited experimental justifications for this division have been Anderson's (1938) and Montgomery's (1953 b) findings that maze exploration is uncorrelated with daily revolutions in an activity wheel.   This is a rather arbitrary basis, however, on which to conclude that the two phenomena represent different underlying mechanisms.   There is, as yet, no evidence to indicate that Y-maze exploration, bar-pressing for light, or problem-seeking behaviour are positively correlated; however, these behaviours have been grouped under the same rubric and probably would continue to be, even in the face of

contrary correlational evidence. This situation has actually already
arisen in the case of activity behaviour. Eayrs (1954) has shown that
activity as measured by wheel turning is uncorrelated with activity as
measured by a stabilimeter cage, yet no one has suggested that they repre-
sent different underlying drives.

There are certain types of evidence which would enable a
meaningful distinction to be made between the activity drive and the
curiosity drive in terms of physiological mechanisms. For example, it
is known that exercise stimulates blood circulation, which in turn removes
waste products and supplies oxygen and nutrients to the musculature. The
absence of activity and consequent reduction in blood flow, could quite
conceivably produce a painful state which would be relieved by activity
resulting in increased blood flow.

Thus, if it could be shown that the activity drive was simply
a reflection of the organism's attempts to avoid pain in the peripheral
musculature, while curiosity behaviour was positively motivated by a need
for a particular type of central stimulation, there would be good grounds
for distinguishing between the two. It is the guess of the writer that
both positive and negative mechanisms will be found to operate in the
activity drive.

Deprivation State and Exploratory Activity

Until 1954, it was generally assumed that water or food
deprivation increased activity. This assumption was based primarily on
the activity wheel studies of Richter (1927), Finger (1951) and Finger & Reid
(1952). The problem was reopened when Campbell and Sheffield (1953), utilizing a
stabilimeter type cage, found that the effect of food or water deprivation was to

decrease activity in an environment which minimized external
stimulation.   If, on the other hand, visual or auditory stimuli were
presented to the deprived animal, he would show significantly more
activity than his satiated counterpart.   Campbell and Sheffield, there-
fore, suggested that the effect of deprivation is not to raise general
activity level, but rather to sensitize the organism to external stimuli.
Their findings, have since been partially confirmed by Strong (1957).
In a more recent study, however, Hall (1956) has taken issue with Campbell
and Sheffield's results and has defended the earlier view that deprivation
states directly increase general activity level.   There are a number of
factors which might explain these differences in results including (a) the
fact that different types of measuring apparatus were used in the two
studies, (b) the somewhat more stimulating environment in Hall's experiments,
and (c) the possibility that Hall's animals had developed a conditioned
running response as a result of the particular feeding schedule under which
they had been placed.   Finger, Reid & Weisner (1957) have described such
conditioned running responses in some detail.

The situation has become equally confused in regard to maze
exploration.   In 1925, Dashiell reported that hungry rats explored more
than satiated rats during a brief period of exposure to a complex maze.
These results were supported by Adlerstein and Fehrer's (1955) similar
finding for food deprivation in an equally complex maze situation.
However, Thompson (1953) and Broadhurst (1957) have reported little, if
any, effect of hunger or thirst on maze or open-field exploration respec-

tively. Finally, Montgomery (1953 a) and Zimbardo and Montgomery (1957) found that substantial decrements in exploratory behaviour resulted from either food or water deprivation. Resolution of discrepancies among these results is complicated by the large number of variables on which the studies differ including sex of experimental animals, feeding schedules, extra-maze cues and maze complexity. All of these variables have been shown to affect exploratory behaviour. Perhaps the most promising explanation has been put forth by Adlerstein and Fehrer (1955) who suggest that the complexity dimension may be the crucial determinant in accounting for the wide disparity in results. There is a rough progression in complexity from the Montgomery studies, through Thompson's and Broadhurst's experiments, to the investigations of Dashiell and Adlerstein and Fehrer. Citing the aforementioned study of Campbell and Sheffield (1953), Adlerstein and Fehrer hypothesize that extremely simple mazes may be equated with an "unstimulating" environment while very complex mazes should provide a sufficiently stimulating environment to evoke the increased activity noted in the stabilimeter cage experiment.

In other situations, the relationship between novelty-seeking behaviour and hunger or thirst is also obscure. Fehrer (1956) has shown that hungry rats will leave a familiar environment to explore a novel one more readily than satiated rats. However, Chapman and Levy (1957) report a reduction in the reinforcing value of novel stimuli as the result of food deprivation. In Skinner-box studies with bar-pressing for light, all varieties of results from depression of response rate to enhancement have been reported to accompany food or water

deprivation. Clayton (1958) and Forgays and Levin (1958) found that deprivation of water and food respectively increased response rate. Hurwitz and De (1958) found no enhancement of bar-pressing with deprivation, and Kling, Horowitz and Delhagen (1956) have reported that a decrement in responding for light is associated with food deprivation.

Habituation

When an organism is confronted with a novel stimulus, it is very likely to demonstrate curiosity. With continued exposure, however, such interest wanes and eventually no further responses are obtained. This widely observed characteristic of animal life has many names; however, for the time being, it will be referred to here as habituation.

Harris (1943) has comprehensively reviewed the literature pertaining to this phenomenon for the pre-World War II era. The animals of that period seem to have consistently produced the expected decrements in exploratory behaviour with the passage of time. In recent years, the situation has become much more complicated. In some experiments, declines in exploratory activity have only been observed to follow continuous exposure to the test situation. Thus, there is a reduction of activity within sessions but complete "spontaneous recovery" is evidenced between sessions (Montgomery, 1953; Harlow and French, 1955; Hurwitz, 1955; Ehrlich & Burns, 1958). On the other hand, there are also reports of declines both within sessions and between sessions for a variety of test

procedures (Schoenfeld, Antonitus and Bersh, 1950; Anderson, 1938;
Berlyne, 1955; Zimbardo and Montgomery, 1957; Glickman, 1958). In
a third group of experiments, declines were observed neither within nor
between testing sessions (Butler and Alexander, 1955; Butler and Harlow,
1954). Finally, there have been a few reports to increased exploratory
activity both within (Welker, 1957) and between (Montgomery, 1953-a;
Williams and Kuchta, 1957) testing sessions. To illustrate the amount
of confusion prevalent in this area, it may be noted that one experi-
menter (Montgomery) has been involved in maze exploration studies which
produced three different results. Actually, there is some reason to
believe that systematic study of this problem may serve to untangle the
situation. For example, Welker (1957) has noted that rats, given a choice
of exploring a new situation or of remaining in a familiar enclosure, demon-
strate increasing exploration both within and between sessions. Rats
forced to explore the same apparatus, on the other hand, show no change
between sessions and decreased activity within sessions. Thus, procedural
variables can be of considerable importance. It also seems likely that
the complexity of the test situation would affect habituation. Thus,
in studies of exploratory behaviour in monkeys, within sessions declines
were noted in a simple activity cage (French and Harlow, 1955) but not in
a visual exploratory apparatus permitting views of a highly variable environ-
ment (Butler and Harlow, 1954). A third procedural variable, likely to
account for failure to find a decrease in some studies, is insufficient
exposure to the test apparatus. Presumably, if an animal were to be
exposed to a situation each day for a year, he would show decrements even

in the most complex apparatus yet used. Finally, in terms of experien-
tial variables, Ehrlich and Burns (1958) have suggested that handling may
exert a crucial influence on between-session declines in maze-exploration
studies. The extent of previous experience in novel situations may also
prove to be a significant variable in determining the rate of habituation.

Satiation and reactive inhibition represent concepts designed
to deal with the same material as habituation. However, each of these
three terms has its reference point in a different portion of the organism,
thereby reflecting some major differences in opinion as to the physiological
substrate of decremental phenomena.

Satiation is generally considered a property of the receptor
organs (Glanzer, 1953), while habituation is usually assumed to take place
somewhere in the CNS (Sharpless and Jasper, 1956). Finally, to complete
the circuit, reactive inhibition places the explanatory burden on the
effector portion of the organism -- primarily the peripheral musculature
(Hull, 1943). In recent years, there has been a tendency for all of these
explanations to approach a common "CNS" ground. As we have seen, the
research on spontaneous alternation forced the proponents of reactive in-
hibition to relinquish the work-produced-decrement notions in favour of
explanations relying on implicit responses which may even be neural in
nature (Berlyne, 1955; Zeaman and House, 1951). Along other lines,
the physiological data showing efferent connections to the sensory
receptors from the cerebrum (Granit, 1955; Kerr and Hagbarth, 1956) must
also inevitably affect explanations based on peripheral sensory adaptation.

It now becomes clear that receptor activity can be modified at the periphery by impulses originating within the brain.

Research on the specific physiological mechanisms under-lying habituation is still in its early stages. However, the recent paper on Sharpless and Jasper (1956) strongly implicates the reticular system in such decremental phenomena. These workers studied habituation to auditory stimuli in the cat using the arousal pattern of the electro-corticogram as their response index. They noted that "repitition of a specific tone, which usually produces long-lasting arousal of a sleeping cat, fails to do so after 20 or 30 trials." Further, bilateral destruc-tion of the auditory cortex failed to influence habituation for specific tones. Section of the brachium of the inferior colliculus, however, increased the speed of habituation and greatly impaired the "tonal specificity of habituation." This data suggests that a mechanism for habituation may reside within the brainstem itself. It is well to keep in mind, however, that such habituation might also be accomplished via the extensive system of fibers to the reticular formation from non-auditory cortex and from the various sub-cortical structures. Support for the latter view may be found in the writings of Pavlov (1941) who noted that: "The investigatory reflex to weak and moderate intensities of external stimulation, in the case of a normal dog disappears by virtue of inhibition after three to five repetitions, and sometimes sooner. In dogs with extirpated hemispheres, there is no inhibition when sufficiently strong stimuli are repeated." A similar increase in resistance to habituation accompanying cortical extirpations was noted by Smith (1941). In this

case, Smith examined the resistance to extinction of optic nystagmus
in guinea pigs subjected to occipital lobe removals, hemidecortication
and total decortication. All of these procedures tended to prolong
the number of trials on which nystagmus was obtained. From these and
other data, Smith concluded that "...the cortex, particularly the frontal
cortex, plays the role of a restraining or inhibiting mechanism in the
nystagmic pattern of the normal guinea pig." French and Harlow (1955)
have similarly implicated the frontal cortex in the habituation of monkeys
in a simple activity cage. On the other hand, there is evidence that
bilateral temporal lobectomy may lead to more rapid habituation in a visual
exploratory situation (Butler and Harlow, 1954), although the same pro-
cedure had no effect in the aforementioned activity cage (Butler and
Harlow, 1954).

An interpretation of these varied results is complicated
by the usual differences in test procedures and species. Sharpless and
Jasper's (1956) identification of the reticular formation as an area
crucial to the habituatory process is highly convincing. However, in
view of the other lesion experiments in this area, the possible significance
of "feedback loops" between the reticular formation and the remainder of
the brain should not be overlooked.

Curiosity Behaviour: Some Theoretical Problems
Most writers have attempted to deal with the various forms of
curiosity behaviour by simply postulating an appropriate drive to account
for their results, e.g., Harlow's manipulatory drive, Butler's visual ex-
ploratory drive, Montgomery's exploratory drive.

The main virtues of such drives seem to be the embarrass-
ment they cause devoted Hullians. As Brown (1955) has shown, however,
most of these difficulties can still be resolved verbally by the die-
hard Hullian as long as the protagonists adhere to the purely behavioural
level. Possibly in order to avoid these problems entirely, one group of
investigators has adopted the accepted "Skinnerian" position of simply
defining their concepts in terms of the operations used to elicit the
behaviour (Premack, Collier and Roberts, 1957). Along the same lines,
Bindra (1958) has argued that assigning a separate drive for each "re-
inforcer" will lead to a long and meaningless list of "names" which really
explain little. He has advocated, instead, a functionalist approach
which emphasizes systematic observation of the behavioural effects of
different sensory stimuli. For example, Bindra and Spinner (1958)
have studied the relative frequencies of grooming, sniffing, freezing,
and other behaviour, as a function of situational novelty.

Some writers, however, have attempted to go beyond the
Skinnerian or functionalist points of view. Berlyne (1950, 1951) has
carried his position further by giving curiosity the status of a primary
drive in a neo-Hullian framework. From this vantage point, he has been
able to make use of the I_r and $_sI_r$ constructs in predicting certain habit-
uatory phenomena (Berlyne, 1955). He has, in addition, avoided the pit-
falls inherent in the "muscular effort" doctrine of I_r by postulating im-
plicit perceptual responses which can presumably build up inhibition at a
neural level.

Somewhat more novel approaches have been advanced by
McClelland and by Hebb. McClelland (1955) has suggested that changes
in sensory stimulation may either prove rewarding or punishing depending
on the magnitude of the change. He hypothesizes that small changes should
prove positively reinforcing, while large changes will lead to negative re-
inforcement. McClelland has further speculated that the reinforcing effects
of small changes in sensory stimulation might be mediated by a mechanism
similar to that underlying reward produced by direct intra-cranial stimu-
lation. This latter idea was based on the finding of Olds and Milner (1954)
that electrical stimulation of the brain of a rat could serve as a reward
in much the same manner as food for a hungry rat.

In a series of articles, Hebb has also proposed an explana-
tion of curiosity behaviour which goes beyond the simple postulation of a
new drive. Thus, Hebb and Thompson (1954) suggest that organisms will seek
an "optimal level of sensory stimulation." Since one of the effects of
sensory stimulation is to arouse the reticular activating system, Hebb and
Mahut (1955) further hypothesize that the organism is seeking to maintain
an optimal level of firing in the reticular formation. It should be
noted that Hebb (1955 a, b) has advanced two somewhat different "optimal
level of arousal" concepts. In one he has postulated an optimal level
of arousal for "cue function" or "performance", and on the other hand he has
proposed that animals will seek to maintain an optimal level of arousal.
It is conceivable that, in a given situation, these two levels would be
quite different. However, Hebb (1955 b) seems to feel that there is a
relationship between the two concepts. The evidence for this relationship

is supplied by studies on the effects of sensory deprivation. In
these experiments, it was shown that depriving individuals of normal
sensory stimulation will lead to both deterioration of performance and
a desire for sensory stimulation of almost any kind. This might be
interpreted as indicating that individuals will act so as to maintain
that level of arousal which is optimal for "cue function". Such a
mechanism would be extremely advantageous for the organism and would fit
in well with evolutionary doctrine.

Both Hebb's and McClelland's approaches are in accord with
data showing curvilinear relationships between stimulus intensity and the
rewarding properties of sensory change. Forgays and Levin (1957) have
demonstrated such a relationship in a situation involving bar-pressing
for light, and Reynolds (1958) has found a similar relationship in bar-
pressing rewarded by intra-cranial stimulation. McClelland might have
some difficulty explaining why turning off a light is apparently unreward-
ing for rats (Hurwitz, 1956, Barnes and Kish, 1957). However, monkeys
will press a bar to turn off a light of moderate intensity (Moon and Lodahl,
1956), and the McClelland hypothesis could undoubtedly be modified to handle
the rat data.

Hebb's optimal-level-of-arousal formulation is also in accord
with a number of recent experiments showing increased exploratory activity
or saccharine consumption in peripherally blind rats (Rhodes and Wyers,
1956, Glickman, 1958; Garcia and Kimelldorf, 1958). Thus, it seems
plausible to assume that, in the absence of visual stimulation, these
animals modified their behaviour in such a manner as to increase the stimu-

lation received through the remaining sense modalities.

Hebb's and McClelland's theories will both eventually
have to be made more specific if any real degree of prediction is to
be extracted from them.   For example, there will have to be some
independent means for specifying amount of sensory change or stimulation
which will produce reward effects in a given situation.   The first
problem here is one of finding a suitable technique for scaling sensory
stimuli.   Kreezer (1958) has recently presented a technique which might
well be adapted to this need, in human subjects at least.   Similarly,
Attneave's (1954, 1957) attempts to scale complex visual stimuli might
also prove valuable in this regard.

In addition, "optimal arousal theory" will have to be modi-
fied in such a manner as to explain why animals habituate to a given
situation rather than grow progressively more active in an effort to
maintain an optimal arousal level.   This can undoubtedly be done.
However, it will necessitate more precise specification of the mechanisms
determining the optimal level of arousal than has been made thus far.

It should be noted that any attempts to meet the above
criticisms with exact specification based on current knowledge would
probably be premature.   The requirements just outlined for the McClelland
and Hebb theories should be viewed more in the nature of programmatic goals
rather than immediate necessities.

Hebb and McClelland have respectively suggested that the
reticular activating system and Olds' reward-structures may mediate the

reinforcing effects of sensory stimulation.   The present study
represents an attempt to subject these speculations to experimental
study.

THE PRESENT INVESTIGATION

At this point, it seems appropriate to review the rationale of the present investigation. Recent research has indicated that visual (Marx, et al, 1955; Kish, 1955; Butler, 1954), auditory (Kish and Antonitús, 1956; Butler, 1957), and proprioceptive or vestibular (Kagan and Burken, 1954) stimuli can serve as positively rewarding events. In view of the fact that all sensory systems send fibers to common regions of the reticular formation (Starzl, Taylor and Magoun, 1951 b; Amassian and Devito, 1954), this system could serve as a "unifying mechanism" at the physiological level. That is, one might assume that the consistently rewarding effects which result from stimulation of diverse sense modalities might all be mediated through the RAS. The RAS has further been shown to project to a wide variety of cortical and sub-cortical regions (Starzl, Taylor and Magoun, 1951 a) and has been clearly implicated in the phenomena of "consciousness" (Lindsley, Schreiner, Knowles and Magoun, 1950) and attentional processes (Lindsley, 1958). Of particular interest is the recent anatomical report (Nauta and Kuypers, 1958) of projections from the mesencephalic portion of the RAS to structures from which reward effects are obtained with intra-cranial stimulation. Thus, there is a possible link between the McClelland and Hebb hypotheses. The rewarding effects of sensory stimulation might well be mediated through reticular activation (Hebb), which, in turn, fires the crucial cells in Olds' "reward systems" (McClelland). The present study constitutes an initial experimental approach to this possibility.

The general procedure involved implanting electrodes in the

mesencephalic reticular formations of rats, and testing the animals in a self-stimulation situation. If reinforcing effects could be obtained from direct stimulation of the RAS via implanted electrodes, it would support the view that this region is capable of mediating the sensory reinforcement underlying curiosity behaviors.

In two animals with electrodes in the posterior tegmentum Olds (1956) obtained no evidence of rewarding effects. In one rat with an electrode in the mesial tegmentum, highly reinforcing effects were noted. This rat pressed quite rapidly with the current on; however, he pressed even faster with the current off. Consequently, the interpretation of the self-stimulation rate with this placement is somewhat obscure. Finally, a moderately reinforcing effect was noted from stimulation of the periventricular gray matter. Brady (1956) has noted a rewarding locus in the reticular formation of the monkey. However, as yet, this has only been reported in abstract form and the details are not known to the writer. One final point should be mentioned. Olds' technique for determining reward effects involved the comparison of a 6 to 12 hour "current-on" period with a one or two hour period with the current off. It was felt that this method might have been too crude to pick up reinforcing effects of a relatively small magnitude. The present study was therefore designed to permit a more sensitive and systematic determination of operant-level bar-pressing.

METHOD

Subjects

Subjects for the present investigation were 40 adult, male hooded rats obtained from the Royal Victoria Hospital colony.

Procedure

Bipolar nichrome wire electrodes 6.0 to 6.5 mm. long were implanted in all animals used in the present study. The electrodes, which have previously been described in detail by Olds and Milner (1954), consisted of two strands of nichrome wire .005" in diameter embedded in a lucite block. The wires were insulated except at the tips, the two exposed ends being separated by approximately 0.5 mm. The operations were performed under Nembutal anesthesia. A Johnson-Krieg stereotaxic instrument was used to place the electrodes in the brain. The electrodes penetrated the skull at a right-angle approximately 6 mm. posterior to bregma and 1.5 mm. lateral to the midline. Three or more days elapsed before testing began.

Testing was carried out in a wooden Skinner box, 12" x 12" x 4", with an aluminum lever projecting from one end. Electrical stimulation could be delivered to the rat in the box through a flexible lead which clipped onto the lucite block. This lead was suspended above the testing box by means of an elastic band so that the animal's movements were not hampered in any way. The source of stimulation was an ordinary 12-volt bell transformer operated from the 110 volt, 60 cycle A.C. power line. The voltage could be continuously varied by means of a potentiometer connected across the secondary winding. All voltage measurements are

given in r.m.s. units. The circuit was so arranged that stimulation could be delivered either coincident with each bar-press or in pulses which were uncorrelated with bar-pressing.

Three groups of animals were used: a self-stimulation (experimental) group, a non-stimulation control group, and a pulsed-stimulation control group. All animals were given one 20-minute session in the Skinner box each day for 10 consecutive days. None of the animals received stimulation on days one through four, to permit the operant levels to be measured.

On days five through ten, the experimental or "self-stimulation" group (N=22) received a half-second burst of stimulation coincident with each bar press. The objectives of this part of the experiment were (a) to determine whether reinforcing effects could be obtained from the midbrain reticular formation, and (b) to localize any such effects as precisely as possible. Because the second objective necessitated using the smallest voltage possible, the following procedure was adopted. A value of 1.0 volt was used on days five and six. If the rate of bar-pressing for a particular rat was higher on these days than the mean response rate for the same rat on days one through four, the voltage was maintained at the same level for that animal during the remainder of the experiment. If no such increment was observed, however, the voltage was increased to 1.5 volts on days seven and eight. Again, if the rate on days seven and eight surpassed that of days one through four, the voltage was kept at the 1.5 level for the remainder of the study. If it was still lower, however, the voltage was raised to a maximum of 2.0 on days nine and ten.

The second group (N=9) was composed of non-stimulated control animals. The rats in this group received no stimulation in the Skinner box at any time.

During the **investigation**, the possibility arose that a moderate increase in bar-pressing rate, observed in the self-stimulation group, might simply reflect general activation due to stimulation rather than a positive seeking of such stimulation. In order to control for this possibility, an additional "pulsed-stimulation" control group was added. Commencing on day five, the animals in this group (N=10) received a 0.5 second burst of stimulation every fifteen seconds throughout the testing sessions irrespective of bar-pressing behavior. The voltage for all animals was 1.0 v. on days five and six, 1.5 v. on days seven and eight, and 2.0 v. on days nine and ten.

Motor effects frequently appeared as concomitants of stimulation. The most common movement was a twisting towards the side of the stimulating electrode. This was particularly pronounced with placements in the vicinity of the red nucleus. Stimulation in or near the central gray matter often produced apparently directed and quite spectacular leaps either out of the box or against a wire mesh roof. All of these motor effects varied in severity as a function of the stimulating voltage. It was, consequently, necessary to reduce the stimulating voltage below the prescribed level on occasion (particularly with the pulsed stimulation group) to prevent an animal from pulling out his electrode.

In four self-stimulation animals that were extremely responsive

to stimulation, an attempt was made to study the effects of various lesions on bar-pressing behavior after the ten days of normal testing. Three of these animals either died after the operation or pulled their electrodes before they could be tested. Such data as could be extracted from the remaining animal, however, will be reported.

At the conclusion of the test procedure, all self-stimulation and pulsed-stimulation rats were sacrificed and perfused with normal saline followed by 10 per cent formalin solution. The brains were removed and frozen sections through the electrode tract were cut at 40 micra thickness. The resultant sections were stained with cresyl violet and the locus of stimulation was determined. (There is one exception to the above procedure. The brain of the rat undergoing successive lesions was fixed in paraffin and alternate sections throughout the brain were stained for both cells and fibers.)

RESULTS

The data summarized in Table 1 indicate that both the non-stimulated and pulsed-stimulation control groups show a significant decline in bar-pressing behavior when the means of the first four "operant level" days are compared with the respective means for days five through ten. The self-stimulation group, on the other hand, shows the reverse trend, although the increase for this group is not statistically significant.

Inspection of the data further reveals that the effects of stimulation in the self-stimulation group are far from consistent. In some cases, stimulation markedly enhances bar-pressing behavior; in others, it has no effect or possibly even depressed the rate of responding. This diversity of effects is reflected in the extremely high variance of the self-stimulation group on days five through ten. The F-ratios for these days between the experimental and control animals are highly significant ($p < .001$), although no such differences were observed during the first four days of testing.

Twelve of the 22 animals in the self-stimulation group showed higher mean response rates on the stimulated days than they had on the operant-level days. None of the nine non-stimulated control animals showed such an increase and only one of the ten pulsed-stimulation animals showed it. Chi-square tests indicate that the self-stimulation group differs significantly from both the non-stimulated ($p < .01$) and pulsed-stimulation ($p < .05$) controls in this respect.

The most plausible explanation of the wide differences in

response to stimulation among the experimental animals rests on cor-
responding differences in the anatomical locus of the stimulating elec-
trode. Although all of the electrodes were aimed at the same general
area of the mid-brain tegmentum, histological examination revealed them
to be widely scattered throughout the mesencephalic portion of the
reticular activating system. In order to investigate the possible re-
lationship between locus of stimulation and response rate, the experi-
mental animals were first divided according to their behavioral responses
to stimulation. The distribution of electrode location within each sub-
group was then compiled. Examination of the response curves for the
experimental animals resulted in the arbitrary division of the animals
into three sub-groups. We shall now turn to an examination of the re-
sponse rates and loci of stimulation within these groups.

Sub-group I (N=4) consists of all animals showing a marked
preference for stimulation. As indicated in Table 2, these animals in-
creased from a mean bar-press rate of 27.4 per session on the operant-
level days to 167.7 per session on the stimulated days. The animals in
this group all showed increased response rates with 1 volt stimulation
and were maintained there for the duration of the study.

It should also be noted that the four animals in this group
tended to show a progressive increase in response rate on stimulated days.
A typical response curve, demonstrating the gradual increment in daily
response level, is presented in Figure 1.

The highly rewarding areas do not appear to be localized in any

one small segment of the reticular formation. The locus of stimulation
for the rat with the highest response rate is in the region of the central
tegmental tract. The next most reinforcing placement is found slightly
dorsal to the above location. The remaining two highly rewarding place-
ments are in the ventro-lateral tegmentum.

Sub-group II (N=8) is made up of animals exhibiting a moderate
increase in bar-pressing under a self-stimulation procedure. Thus, they
increased from a pre-stimulation mean of 18 presses per session to a mean
of 29 presses per session on the stimulated days. Examples of response
curves obtained from this group are presented in Figure 2. The data for
the individual animals in sub-group II has been summarized in Table 3.

Sub-group III (N=10) comprises the remainder of the self-stimu-
lation group. These animals all showed decrements in response rate of
varying magnitude when the stimulated days were compared with the non-
stimulated days. The group as a whole declined from a mean of 31.9 presses
per session to a mean of 10.9 presses per session. The data for the in-
dividual rats is summarized in Table 4. As may be seen, in those cases
where stimulation had no effect, the site of stimulation was most often
in the central and dorso-lateral portions of the activating system.
In rats 18 and 19, the loci of stimulation were near the red nucleus
and central gray matter respectively. However, the electrodes in these
cases were about 1 mm. posterior to the sites of stimulation for sub-
groups I and II where rewarding effects were obtained. Rat number 15,
though technically included in the non-rewarding group, did show signs
of reinforcement when the stimulation voltage was increased to 2.0 on

days 9 and 10. This was marked by a sudden increase in bar pressing
rate to a level which had not been reached since day 2. In view of
this, its data may not actually conflict with those obtained with sim-
ilar placements in sub-group II.

The results of the above anatomical breakdown are summarized
in Figure 3. Reinforcing effects were found in two general regions.
The first ranges from the central gray matter to the dorso-medial aspect
of the red nucleus and includes the central tegmental tract. The second
region is located in the lateral tegmentum dorso-lateral to the red
nucleus. Subjects 2, 6, 7, 30, 51, 54, and 64 are included in the for-
mer area, while 1, 12, 13, 56, 58, 63, and 83 are found in the latter.

A few notes are in order. It would appear that relatively
small changes in locus can produce profound changes in bar-pressing be-
havior within this system. Thus, the electrode in rat number 11, which
showed no evidence of reinforcing effects, seems to be but slightly
dorsal to the placement in rat number 2, which showed very marked effects.
Large differences in bar-pressing behavior accompanying small differences
in locus of stimulation are similarly found between rats 58 and 83 and
between rats 1 and 15. There are, however, one or two differences in
response rate which are not easily ascribed to differences in site of
stimulation. Thus, rats 13 and 63 appear to have been stimulated in much
the same area; yet the former showed a clear cut reinforcing effect
while the latter did not. A discrepancy such as this may be due to limi-
tations in the accuracy with which the sites of stimulation can be

identified histologically. However, it may also reflect differences in subjects or stimulating current.

Because of the small number of animals in the pulsed stimulation group, it is difficult to make any systematic anatomical analysis. One (activated) rat showed increased bar pressing during the last six stimulated days, while three animals appear to show very sharp decrements in bar pressing on stimulated days -- this becoming particularly noticeable as the voltage was increased. The lone activated animal was stimulated in the central tegmentum at the level of the red nucleus. The three "low rate" animals were stimulated in areas adjacent to the central gray matter and red nucleus where rewarding effects were noted in the self-stimulation group.

Two days after the last regular testing session, an attempt was made to produce a bilateral septal lesion in rat number two by means of electrocoagulation. As may be seen in Figure 4, the lesion, though extensive, spared the anterior septal area, while encroaching posteriorly on the columns of the fornix, laterally into the caudate nucleus, and dorsally into the corpus callosum. The operation led to the usual septal hyper-reactivity, although this had largely disappeared one week later when the animal was again placed in the Skinner box for testing.

In two testing sessions conducted at this point, the rat averaged 470 presses per session, which seems to form a continuation of his pre-operative curve (see Figure 1).

Two days later, further bilateral lesions were made in the ventral

portion of the temporal lobe (see Figure 4). The rat was tested twice
after this operation, once on the day immediately following the operation
and again some five days after that. He pressed 484 times and 1087 times
in the respective 20 minute sessions. A third set of lesions was then
made in the hypothalamus. However, these lesions resulted in a severe
motor deficit, and the animal was in a generally poor condition. In
a test conducted the day following the hypothalamic lesion, the animal
only pressed 27 times, but the interpretation of this decrement is quite
unclear.

DISCUSSION

The results of this study support the hypothesis that reticular formation stimulation can serve as an effective reinforcer. They are, therefore, compatible with the view that the rewarding effects of sensory stimulation are mediated, in part at least, through activity induced by sensory stimuli in the arousal system of the brain stem.

An unexpected result, however, was the wide range of self-stimulation rates obtained from electrode loci within the mesencephalic portion of the activating system. Stimulation in this region was highly reinforcing for some subjects, moderately so for others, and had no clear effect in a third group. Small differences in the locus of stimulation appear to offer the most promising explanation of the result. However, this, in turn, necessitates the postulation of a hitherto undemonstrated degree of functional localization within the mesencephalic activating system in general and the reticular formation in particular. There is no doubt that gross activation of the electroencephalogram (EEG) can be achieved from large areas of the rat brain stem (Caspers and Winkel, 1954). In a previous study carried out by the writer, there was occasion to observe the effects of stimulation of the mesencephalic portion of the RAS on the cortical EEG of the rat. The three animals tested in this fashion were all aroused from the resting state (both behaviorally and electroencephalographically) by the stimulation, although the electrode loci ranged from the central gray, to the area dorso-lateral to the red nucleus. The results of the present investigation suggest that, in addition to the gross EEG activation, there are subtle behavioral effects

which are much more strictly localized. It seems appropriate, therefore, to examine the results of the present study in the light of current anatomical and physiological knowledge regarding localization within the activating system of the brain-stem. There are two limiting factors which should be kept in mind during the ensuing discussion. First, nearly all of the physiological-anatomical data to be cited are based on studies with cats. As Brodal (1957) has pointed out, the organization of the activating system in other species may prove to be quite different. Second, the anatomical differences among the three sub-groups in the present study are relatively crude because the region of stimulation surrounding the electrodes undoubtedly occupies a considerable area relative to the total extent of the activating system in the rat brain-stem. Nevertheless, some interesting correlations appear between the self-stimulation data and the physiological-anatomical information.

Electrode loci leading to reinforcing effects in the mesencephalic activating system of the rat were found in two regions; the first was in the vicinity of the central tegmental tract, the second dorso-lateral to the red nucleus. In their examination of the brain-stem of the cat, Starzl, Taylor and Magoun (1951 a) similarly found two discrete areas from which activation of the electrocorticogram was most dependably accomplished. One such area is in the general region between the central gray matter and the red nucleus. This is apparently analogous to the first reinforcing region located by the self-stimulation technique in the rat. The second sensitive area denoted by Starzl, Taylor and Magoun involves the region surrounding the brachium of the inferior colliculus

and the medial lemniscus. This would appear to be somewhat more lateral
than the second reinforcing region found in the present study. However,
the general similarity of the breakdown into separate medial and lateral
regions, achieved independently by the physiological and behavioral tech-
niques, is certainly worthy of further investigation.

It is also interesting to examine the self-stimulation data in
the light of recent work by Nauta and Kuypers (1958) indicating a certain
degree of localization in the cat tegmentum along the rostro-caudal axis.

These investigators have found that the majority of reticulo-
thalamic fibers originate in the medulla and pons. On the other hand,
the caudal portions of the mesencephalic reticular formation contribute
fibers terminating in the lateral hypothalamic region, the pre-optic
area and the septal nuclei; while the rostral mesencephalic tegmentum
is the only source of projections to the basal ganglia. In the present
study, the majority of the electrodes were located in the rostral mesen-
cephalon at the level of the red nucleus. No evidence of reinforcing
effects was found in the three animals with electrodes posterior to this
region. Olds (1956) has similarly reported an absence of reinforcing
effects in his (three) tegmental placements posterior to the medial
geniculate, at which level he found the only reinforcing tegmental place-
ment. The self-stimulation data are, therefore, in accord with the
presence of rostro-caudal localization within the tegmentum of the rat
analogous to that found in the cat by Nauta and Kuypers. However, it
would be dangerous to infer that rewarding electrode placements in the
present study are distinguished from non-rewarding posterior placements

by virtue of the additional connections of the former group with the basal ganglia. Considering the small number of animals involved and the dangers inherent in moving from one species to another, this must again remain a possibility for further research.

On the basis of extensive anatomical data, Brodal (1957) has recently drawn a new picture of reticular formation organization. Thus, he distinguishes between a lateral "sensory" zone and a medial "effector" zone. The lateral zone apparently receives the majority of afferent collaterals from the specific sensory systems. Impulses reaching the lateral zone may subsequently be relayed via internuncials or medially running axons to the "effector" zone. This region, which comprises roughly the medial two-thirds of the tegmentum, gives rise to the vast preponderance of ascending fibers. Again, drawing on recent anatomical researches (Brodal and Rossi, 1955; Torvik and Brodal, 1957; Scheibel and Scheibel, 1958), Brodal concludes that both ascending and descending ɣ transmission from the reticular formation proceeds largely via long axon fibers, rather than by a short-axon multi-synaptic process as was assumed hitherto.

The material presented thus far, suggests that the reinforcing effects of reticular stimulation are mediated via long axon fibers originating in discrete areas of the activating system and projecting to the various sub-cortical structures constituting Olds' "reward systems" (Olds, 1956). With regard to those reward effects obtained with ventrolateral placements, it seems likely that the activity must first be transmitted medially. The results of the present study would further suggest

that such medially running axons or internuncials, capable of firing the "reinforcing" ascending fibers, exist primarily in the ventral portions of the system since similar reward effects did not occur with more dorsal placements.

In addition, it seems unlikely that any reward network will turn out to be a simple chain-like affair where severing one of the links disrupts the entire system. In the one animal from which such data could be gathered, the reinforcing effects of rostral tegmental stimulation persisted undiminished following destruction of portions of the septal area, caudate nucleus, ascending columns of the fornix, corpus callosum, and temporal lobe. Systematic use of this combined stimulation-lesion technique could provide valuable information about the functional organization of the reinforcing pathways. It would, of course, be unwise to neglect the role of the cortex in the operation of such a reward system. By means of the numerous feedback loops which have been demonstrated to operate between the cortex and sub-cortical centers (Adey, Segundo and Livingston, 1957), the cortex is in an excellent position to regulate the activity of such lower structures.

There are two variables, apart from locus of stimulation, which may need to be taken into account in explanations of the present results. The first concerns hereditary-experiential factors. These might have led to significant differences in the microstructure of the brain such as those discussed by Lashley (1947). The other variable is the stimulating current, but the significance of this is doubtful.

With regard to the former possibility, it can only be stated that the previous work on self-stimulation (Olds, 1956) supports the view that, within specified anatomical loci, response to stimulation is roughly the same. On the other hand, it does seem plausible to assume that occasional differences, of relatively small magnitude, between the animals in sub-groups II and III might be due to variation in the response of individual subjects to stimulation. In psychological experiments, involving the behavior of the whole animal, a certain amount of variability from one animal to another is probably unavoidable.

In relation to the problem of stimulating current, Reynolds (1958) has shown that increases in current are often accompanied by co-incident increases in rate of responding for stimulation. However, current measurements taken on a sample of seven rats from sub-groups I, II and III disclosed no simple relationship between stimulating current and response to stimulation. Thus, we can rule out the possibility that variations in stimulating current accounted for the major differences in the effects of stimulation observed in the present study.

From the above remarks it appears that differences in the micro-structure of the brain and stimulating current, although probably accounting for some of the inter-animal variability, cannot explain the major differences in response to stimulation. Any complete explanation of the results of the present investigation, necessitates the postulation of a considerable degree of functional localization within the activating system of the rat.

To return to the issue which initiated the present investigation, reinforcing effects of a similar magnitude to those obtained with light reinforcement were occasionally found in the present study (sub-group II). On the other hand, in many cases, the reward effects were either absent entirely or of too great a magnitude to be analogous to the ordinary external sensory reinforcers. It is clear, however, that the pattern of reticular excitation induced by even a simple burst of light would be totally different from that produced by stimulation through the electrodes used in the present experiment. Thus, light stimuli might be expected to produce a complex, composite effect resulting from the activation of both rewarding and non-rewarding cells throughout the reticular substance.

In recent years, psychologists have borrowed from the physiologist certain concepts relating to a diffuse projection system which controls the organism's level or arousal or activation. Anatomical and physiological data previously cited in the present paper indicate that the organization of the RAS is not as simple as was first thought. The results of the present study supply behavioral data in accord with some of the more recent information gathered by other disciplines. Psychologists have thus far made good use of the early simplified view of the RAS. Ultimately however, it seems likely that they will have to take into account the details of reticular formation function, as well as the gross aspects, in the construction of physiologically oriented theories.

SUMMARY

Recent studies of curiosity and novelty-seeking behavior have shown that sensory stimulation can serve as a reward. The suggestion has been made that such reward effects are mediated through activity, induced by sensory stimuli, in the reticular activating system (RAS). To investigate this suggestion, rats with electrodes implanted in their RAS's were tested in a self-stimulation situation. Electrical stimulation delivered to some portions of the RAS was found to constitute an effective reward, although the magnitude of the reward effects varied greatly from one animal to the next. Stimulation was not rewarding in other parts of the RAS. In a control group, stimulation delivered independently of bar-pressing did not increase response rates. Further analysis of the results indicated that differences in locus of stimulation could best account for these findings. This necessitated the postulation of a considerable degree of functional localization within the RAS.

The findings support the suggestion that the RAS mediates sensory-reward. However, the RAS does not appear to function as diffusely as hitherto supposed.

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TABLE 1

Mean Response Rates for Experimental and Control Groups
on Stimulated and Non-stimulated Days.

| Group | $\underline{N}$ | Days 1-4 | | Days 5-10 | |
		Mean Responses per Session	$\underline{s}$	Mean Responses Per Session	$\underline{s}$
Experimental (Self-stimulation)	20^a	25.4	16.4	49.8	63.4
Control I (Non-stimulated)	9	28.2	13.5	16.2	10.2
Control II (Pulsed-stimulation)	10	46.9	26.3	23.4	20.9

[a]Two rats, that lost their electrodes on days 9 or 10, are not included in this group.

TABLE 2

Bar-pressing Rates for Individual Rats in Sub-Group I

Rat	Operant Level Days 1-4	Self-stimulation Rate Days 5-10
1	24.25	179.33
6	40.50	220.66
2	18.00	132.83
58	27.00	137.83

TABLE 3

Bar-pressing Rates for Individual Rats in Sub-Group II

Rat	Operant Level Days 1-4	Self-stimulation Rate Days 5-10
7	30.75	45.00
12	4.50	17.50
13	10.50	39.17
30	29.00	37.00
64	9.50	29.67
51	11.50	21.17
54	7.75	8.33
83	31.50	33.50

TABLE 4

Bar-pressing Rates for Individual Rats in Sub-Group III

Rat	Operant Level Days 1-4	Self-stimulation Rate Days 5-10
11	12.00	5.00
15	51.25	16.00
18	40.25	6.50
19	65.00	27.17
33	40.00	11.17
55	15.50	5.33
56	11.25	4.00
63	27.75	18.33
21	40.30	2.50[a]
60	15.30	12.50[a]

[a]Based on only four days. These animals pulled their electrodes on days 9 or 10.
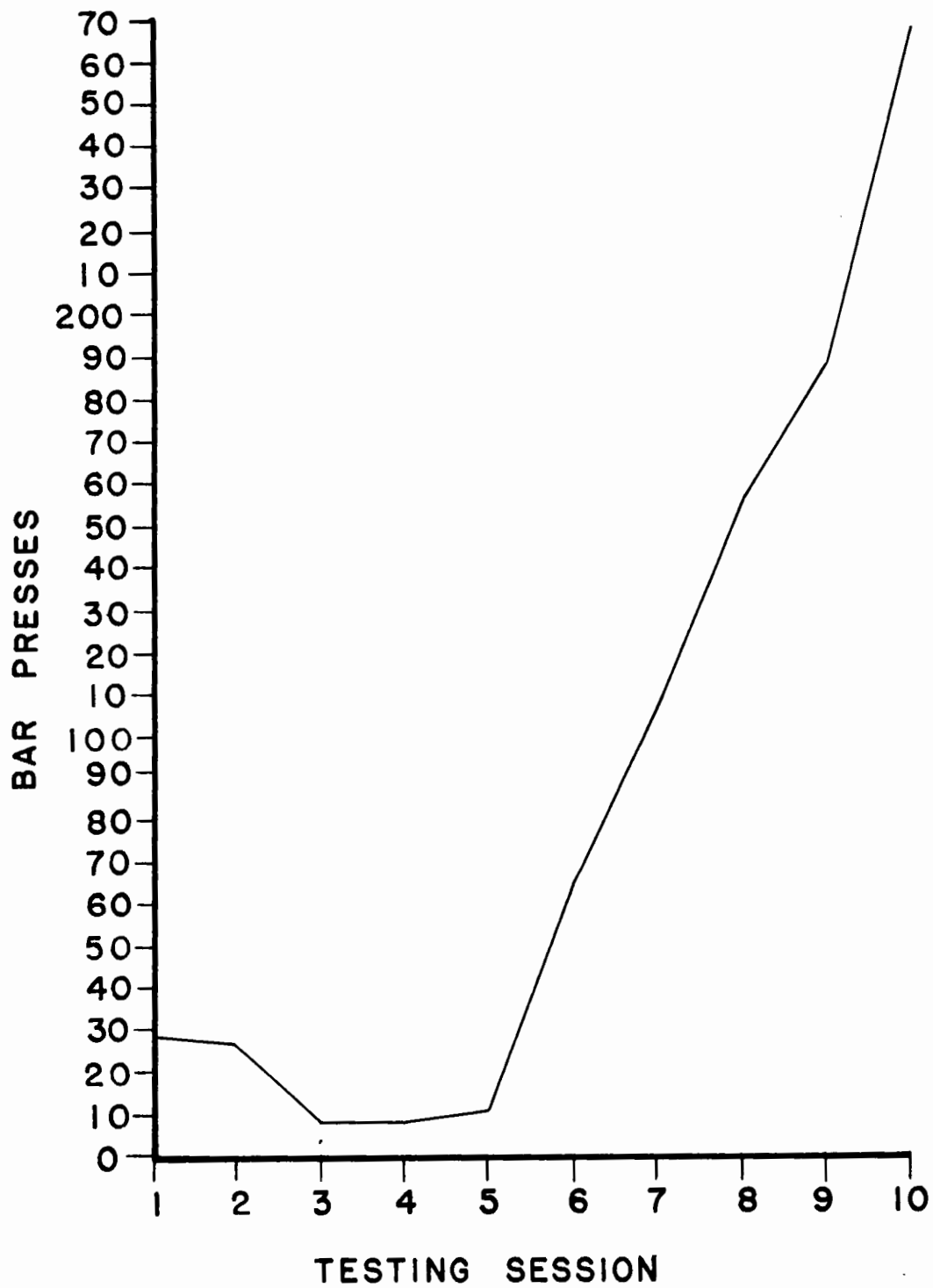
Figure 1. Daily bar-pressing rate for rat number 2.
One-volt stimulation was introduced on day five.
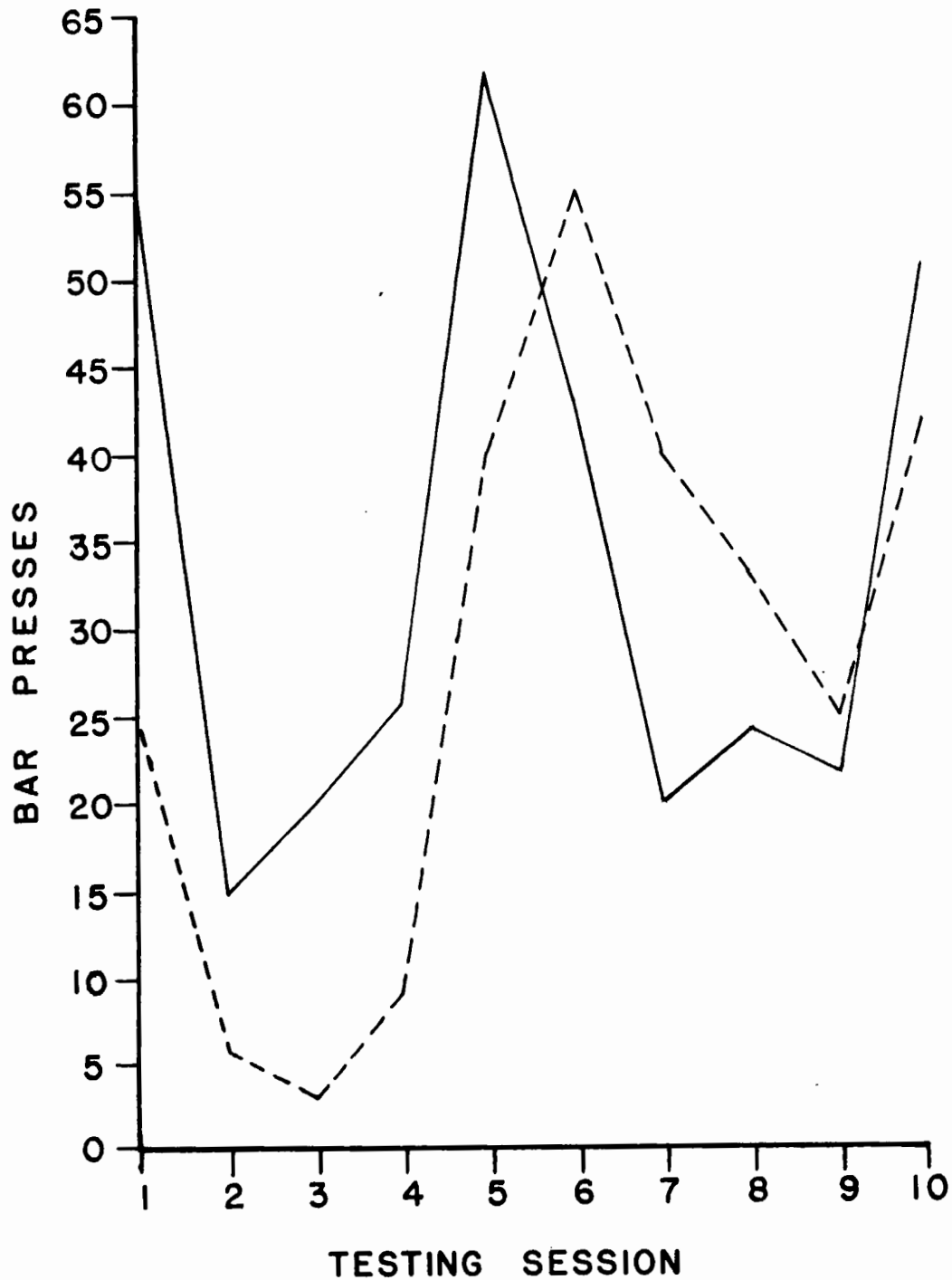
Figure 2. Bar-pressing rates for rats number 13 and 30. Rat

number 13 is represented by a dotted line, rat number 30

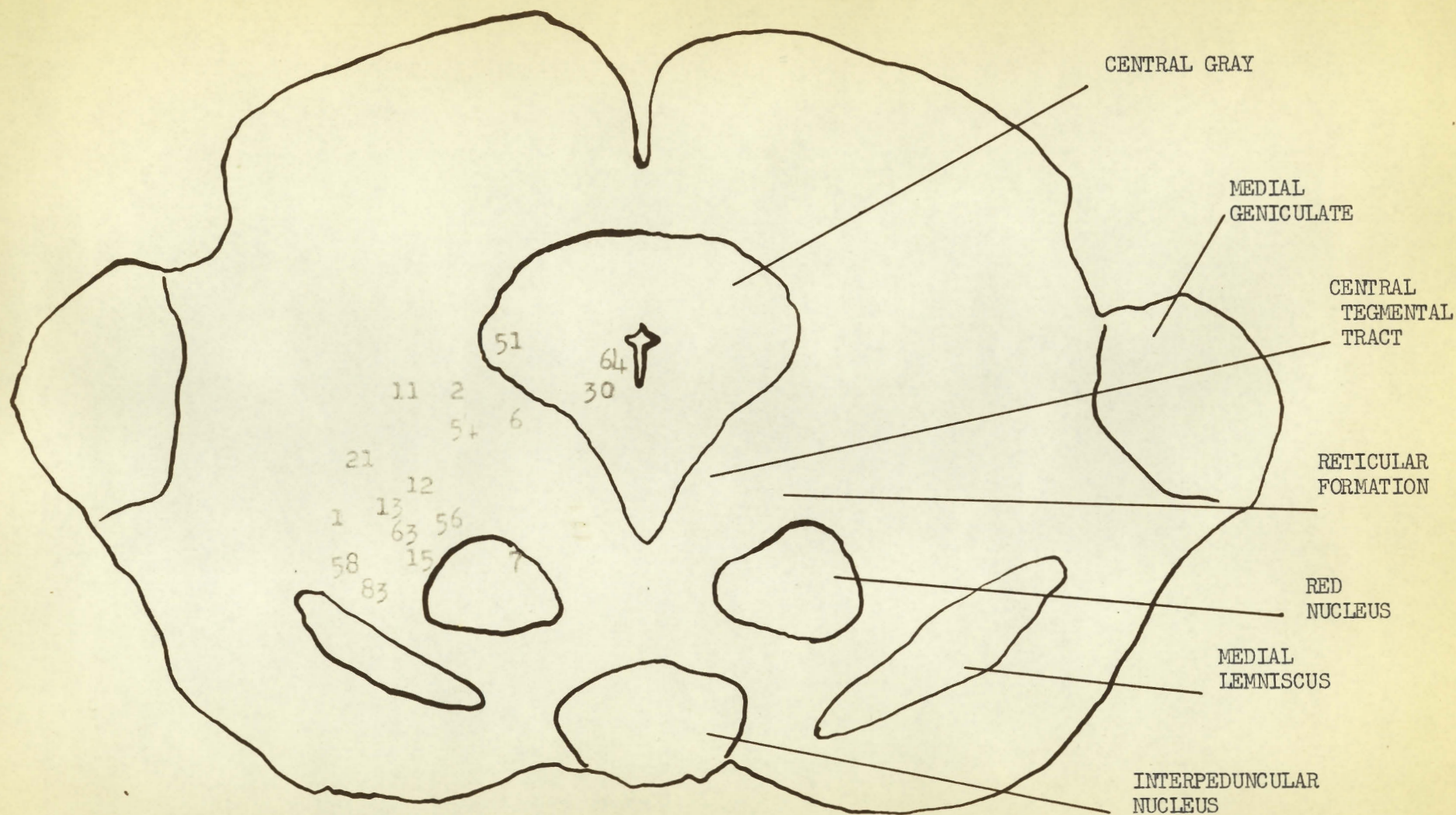by a solid line. One-volt stimulation was introduced

on day five.

Figure 3A. Electrode Locations (Anterior Group)

Numbers indicate position of electrode tips in rats referred to in Tables 2, 3, and 4.
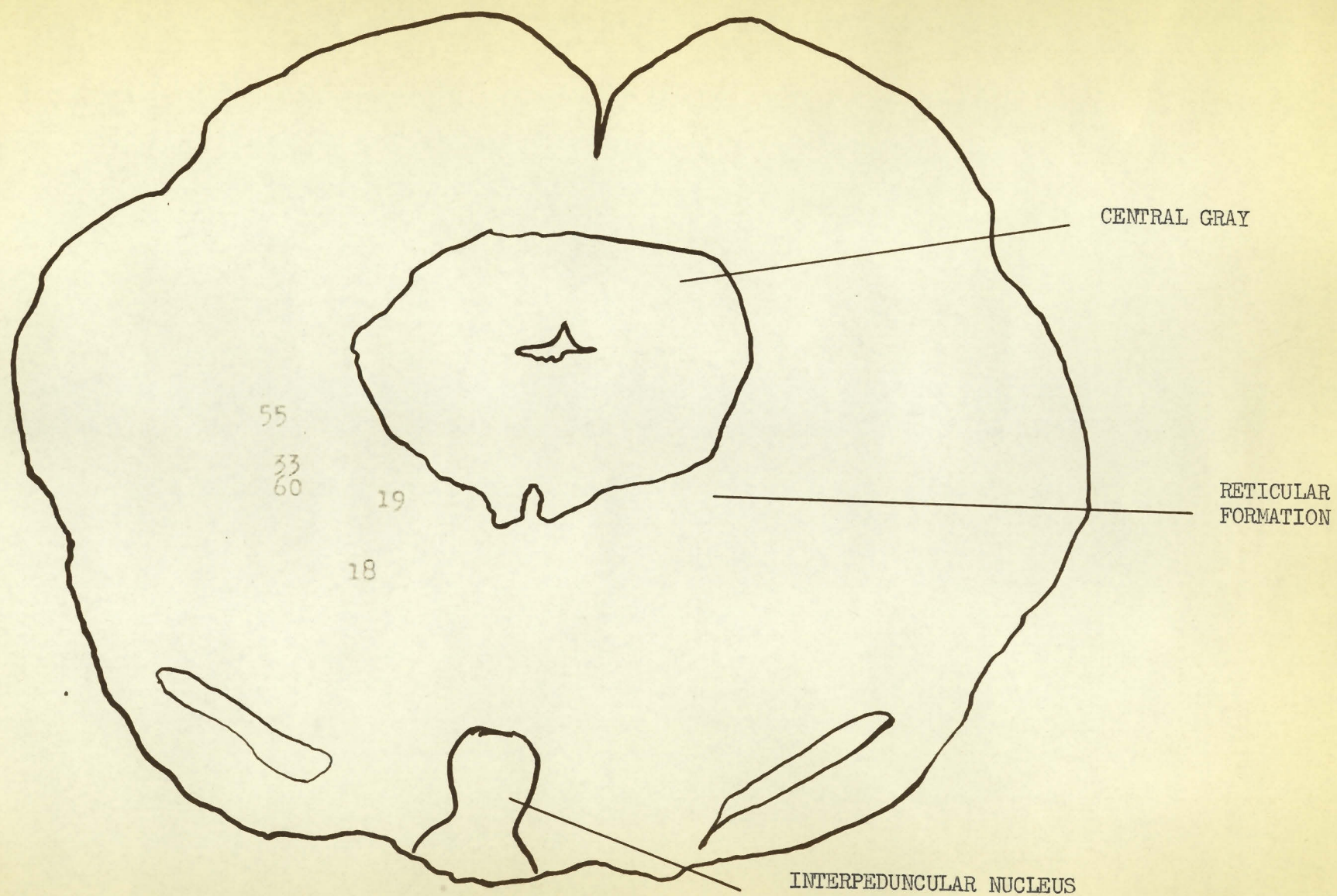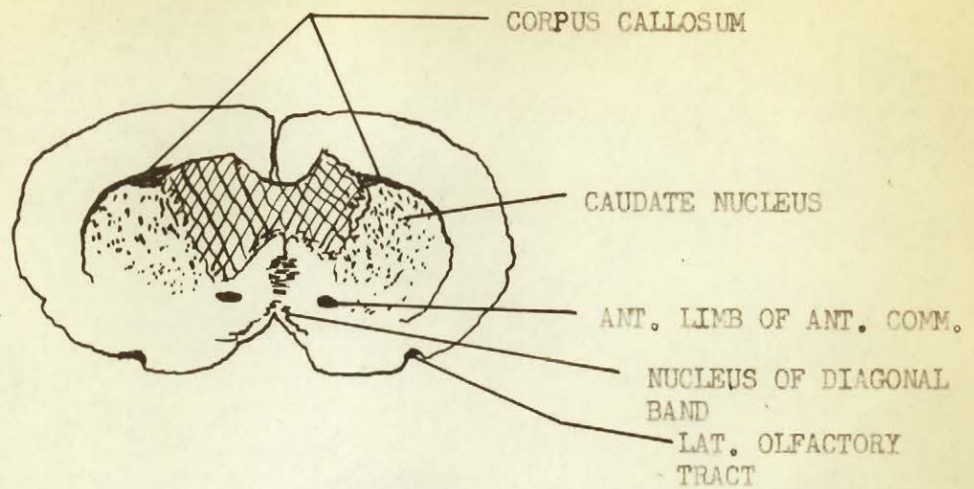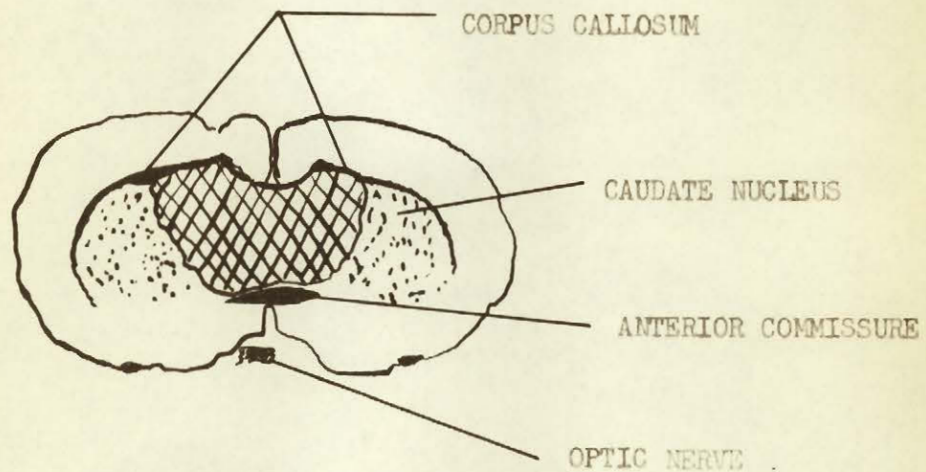
CENTRAL GRAY

RETICULAR
FORMATION

INTERPEDUNCULAR NUCLEUS

Figure 3B. Electrode Locations (Posterior Group)

CORPUS CALLOSUM

CAUDATE NUCLEUS

ANT. LIMB OF ANT. COMM.

NUCLEUS OF DIAGONAL
BAND
LAT. OLFACTORY
TRACT

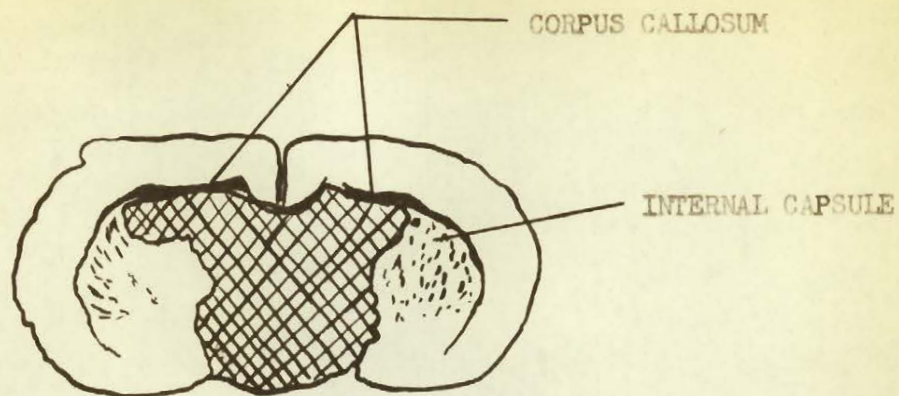Area destroyed by first lesion

CORPUS CALLOSUM

CAUDATE NUCLEUS
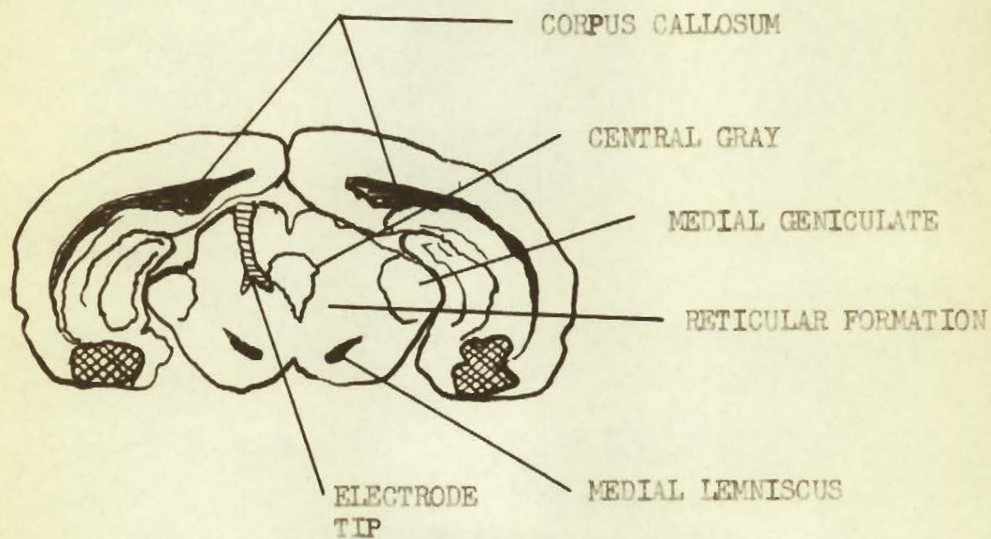
ANTERIOR COMMISSURE

OPTIC NERVE

Area of overlap of first and third lesions

Figure 4A. Extent of lesions in rat No. 2

Cross-hatching indicates area of destruction

Area destroyed by third lesion

Area destroyed by second lesion

Figure 4B. Extent of lesions and electrode locus in rat No. 2.