THUMPING BEHAVIOUR IN THE RABBIT

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By

STEPHEN LAWRENCE BLACK, B.SC.

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AUTHOR: Stephen Lawrence Black, B.Sc. (McGill University)

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SCOPE AND CONTENTS: Electrical stimulation of areas in the diencephalon and central grey of the conscious rabbit produces a response of thumping the ground with the hindfeet. The response is not elicitable from the neocortex, striatum or internal capsule. Thumping movements occur mainly after offset of the eliciting stimulus and the likelihood of a response decreases regularly with time, suggesting the decay of a central excitatory state.

Central stimulation which produces thumping behaviour tends to be aversive in tests for self-stimulation. Further, the behaviour can be elicited by peripheral electric shock. Therefore thumping behaviour may be a sign of fear in the rabbit.

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Figures

INTRODUCTION

Charles Darwin(4), in "The Expression of the Emotion in Man and the Animals", observed

> "Rabbits stamp loudly on the ground as a signal to their comrades; and if a man knows how to do so properly, he may on a quiet evening hear the rabbits answering him all around. These animals, as well as some others, also stamp on the ground when made angry."

More contemporary observers have also reported this behaviour pattern (1, 17, 19). Following Darwin, thumping has usually been referred to as a warning signal for the species. However, it occurs rarely in situations where it may be closely observed. For example, one intensive study of enclosed rabbit populations for 400 hours(17) failed to report a single occurence of thumping. In addition, no experimental study of thumping in the rabbit has been published. Therefore, there appears to be no good evidence to support these suppositions concerning the elicitation and function of thumping, in spite of the fact that these hypotheses have now become folklore (20).

Recently Vanderwolf (personal communication), in an exploratory study, found that thumping may be elicited by electrical stimulation of the unanesthetized rabbit brain. The present research has attempted to utilize this finding to investigate the response of thumping in detail. In particular, it was hoped that the use of this method of elicitation of thumping might allow delineation of the central nervous system structures involved in the response and some indication of what the function of this behaviour might be.

ANIMALS AND PROCEDURE

Data were obtained from 32 New Zealand White male rabbits, weighing between four and eight pounds at the start of the experiment. The Ss were anesthetized with pentobarbital sodium. Four (occasionally three or five) bipolar electrodes were implanted stereotaxically and cemented in place with dental acrylic moulded over stainless steel screws fixed in the skull. Penicillin was given immediately post-operatively, and in some cases, during recovery.

Electrodes were made from twisted Nichrome wire 0.010 inches in diameter, and soldered or crimped to small Amphenol connectors, which were then cemented with dental acrylic to form a rigid assembly. In succeeding steps, the electrodes were insulated with Epoxylite, baked, the junction of wire and connector coated with Insulex, and tested with ohmmeter and saline solution for conductance, short-circuits, and leaks. Before implantation the electrodes were cut to size, scraped free of insulation for approximately 0.5 mm. from the tip, and the tips separated by 0.5-1.0 mm.

The box used for behavioural observations measured 31 x 31 x 28 inches high, except on the side where the experimenter sat, which consisted of a Perspex window 9 inches high. A removable barrier could raise this side to the height of the others if necessary. The floor of the box was covered with Absorb-dri, and food, water, paper strips, and wood were always present.

Stimulation was carried out using a Grass model S4 stimulator, set for biphasic square pulses of 0.5 msec. duration. Testing was not started until at least 10 days after the surgery. The following stimulation settings were used, in ascending order:

5 c/sec.	6, 8, 10, 15. V.
20 c/sec	4, 6, 8, 10, 15. V.
100 c/sec.	1, 2, 4, 6, 8, 10, 15. V.

These represented scale settings and not measured voltage. Stimuli were usually delivered for 15 seconds with at least a one minute interval between presentations. With each presentation the stimulus setting was increased one step, until a response was elicited. The stimulus train was then repeatedly presented at this setting until the activity could be identified, and again repeatedly presented at higher settings. Polarity was switched after each presentation of the stimulus train. Testing was discontinued whenever an excessively strong motor pattern occurred. If a seizure was elicited the sequence was terminated and the site retested after an interval of at least 24 hours.

Thumping was elicited from 83 of the 131 sites tested. In order to have baseline values for subsequent experiments, 38 electrodes in 17 rabbits were tested further to determine thresholds. A threshold trial consisted of a series of stimulus train presentations in one-volt increments, terminated as soon as thumping was elicited. Trials were spaced at least an hour apart, or in the case of a seizure, 24 hours apart. Presentations were 15 seconds long except where severe motor effects made shorter stimulus train durations necessary. On the preliminary trial, stimulus parameters were initially set a few volts below those at which thumping had first been elicited. Polarity was switched with every stimulus presentation. The function of the preliminary trial was to approximate the threshold so that it could be reached on succeeding trials with a miniumum of stimulation, and thus avoid variability. If thumping could not be elicited within three trials testing at that point was discontinued, and the site labeled "unreliable".

Following a successful preliminary trial, threshold testing began. The initial stimulation setting for each trial was one volt below that at which thumping had been elicited on the previous trial. A threshold was calculated as the median of the voltage settings at which thumping had first been elicited for a number of trials. However, sites from which thumping was elicited on less than 50 per cent of the trials, or whose thresholds on individual trials varied more than a few volts from the median, were considered unreliable. The number of trials was not fixed so that sites with variable thresholds could be tested more thoroughly. The median number of trials given was five.

After completion of further test, a three-trial re-test of threshold was carried out for 15 placements in which reliable thresholds had been determined.

Thump Recording

Thumping elicited by the above stimulation procedure appeared to become less and less frequent with time after termination of the stimulus. In order to study this apparent decay of the tendency to emit thumps and to determine whether a relationship existed between number of thumps and the location of points eliciting thumping, the following procedure was initiated.

The apparatus was modified to allow control of the on switch of the stimulator by a Hunter timer. Thumps were recorded on a Gerbrands event marker by manually depressing a key each time the response was observed. The same channel also recorded the onset and offset of the stimulus.

Preliminary testing was carried out in a single rabbit (16E) in which a threshold had not been determined. Twenty electrode placements (in 13 rabbits) for which a threshold had been determined were then tested, with voltage set at 1.5 times threshold. The rabbit was first placed in the box for a few minutes with the event marker running. The Hunter timer was then switched on to begin stimulation for a fixed time interval, usually 15 seconds, but occasionally for a shorter period if a strong motor pattern was elicited. All thumps were recorded until none had been emitted for some time, usually a few minutes. The rabbit was then left in the box for a few more minutes before being returned to its cage. A minimum of five trials were given, at intervals of not less than one hour. Animals which responded with large numbers of thumps, or had other interesting properties, were usually given further trials.

Histological Procedure

When all stimulation tests (including reinforcement testing, which is described in a later section) were complete, each rabbit was anesthetized and perfused with 10 per cent formalin. Frozen sections were cut at 40 μ and stained with either cresyl violet or thionin. Using the atlas of the rabbit brain by Fifková and Maršala(6), the electrode tips were localized on two separate occasions, without knowledge of the behavioural results.

Results

Centrally-elicited thumping consisted of an abrupt co-ordinated movement of both hind limbs. The feet were raised and brought downward sharply on the ground to produce the characteristic "thump" sound. The response generally occurred while the rabbit was standing motionless, apparently very alert, but was sometimes observed while it was moving. The behaviour was sometimes accompanied by a brief grunt. Initiation of thumping occurred most commonly within a few seconds after cessation of stimulation, and continued for a variable period of time. The behaviour rarely occurred during stimulation. Spontaneous thumping was almost never observed.

Stimulation also produced a variety of other responses, some of which were more frequently associated with thumping than others. Activities most often elicited from placements producing reliable thumping include freezing, alerting, escape, orienting movements of the head, and searching. Searching refers to slow locomotion of variable direction, with sniffing and orientation to environmental objects. Activities elicited from placements which fail to produce thumping include turning the head to a fixed position, chewing, alternating up and down movements of a single fore paw, and trembling about the face, ears and vibrissae. Activities associated with placements eliciting unreliable thumping include orienting movements of the head, pupillary changes, seizures, alerting, escape, and crouching. Turns were frequently elicited within all categories, but in particular from unreliable thumping placements.

Thumping was also elicited, in experiments to be described later, through peripheral shock administered with sub-dermal electrodes. This finding that aversive peripheral stimulation may produce thumping introduces the possibility that the thumping attributed to stimulation of central structures may be due instead to secondary aversive consequences of strong motor patterns elicited by the stimulation. That this is not a likely hypothesis is suggested by the fact that thumping was not elicited in a number of cases where very strong motor patterns have been observed.

For example, in one animal, stimulation produced chewing, and turning the head to the side, then up and over the back, until the head was pointing straight up. With stronger stimulation, the rabbit began making rapid turns, pivoting on its hind paws. The final stimulation at 15 V. was terminated before the usual 15 second period was complete because of the severity of the response. Another animal responded at 20 cps with an elongation of the body and strong trembling. At 100 cps sudden backing up was produced, and stimulation was terminated, again because of the severity of the response. Thumping was not elicited from either of these placements. On the other hand, one animal responded to stimulation, after a few seconds delay, by sinking slowly and smoothly into a semi-crouch as though going to sleep, with eye-blink, pupil constriction, and a few jerks of the body. This animal produced reliable thumps during stimulation. The protocol on another placement states "at low values, frequently no motor at all, yet thumps at offset".

The data on thumping were classified into three categories, which are plotted as a function of anatomical location in Figure 1. Reliable thumping points are those for which a stable threshold was found. Unreliable thumping points are those from which thumping was elicited, but a stable threshold could not be found. Most commonly, electrodes were placed in this category because thumping could not be elicited on re-testing, or was elicited infrequently. No thumping points are those from which thumping was never elicited during initial behaviour testing, and were therefore not re-tested. Omitted from Figure 1 are a number of points from whichthumping was elicited during preliminary work, but which were not tested further.

Four electrodes placed within the hypothalamus and five electrodes within the midline region of the thalamus were found to produce reliable thumping. The behaviour was also reliably elicited from two sites within the central grey, and from two sites bordering this area, within commissural fibers. Negative or unreliable sites were not found within these areas. Therefore, these structures are unambiguously implicated in thumping behaviour. Other points yielding reliable thumping on stimulation were found in or near the reticular formation, superior colliculus, fornix-fimbria region, and septum.

Unreliable thumping placements were found within the septum, amygdala, and lateral thalamus. The behaviour was never elicited from the cortex, corpus callosum, anterior commissure, striatum or internal capsule, suggesting that these structures may not be involved in thumping.

No relationship was found between thresholds and the anatomical distribution of sites at which they occured. Median value of thresholds found at 20 c/sec. was 5 V., with a range from 2 to 10 V. (N = 17). For thresholds found only at 100 c/sec., the median voltage was 3, with a range from 3 to 6 V. (N = 5).

Re-test thresholds for eight electrodes tested within 8 days after the original threshold determination ranged from - 2 V. to + 2 V. of their previous values, with a median change of + 0.5 V. Seven electrodes re-tested within 34-67 days after the original test ranged from 0 to + 3 V. of their previous values, with a median change of + 1.0 V. The thresholds, therefore, were both reliable and stable.

Thump Recording

The number of thumps elicited by stimulating at 1.5 times threshold voltage varied greatly with electrode location. Midbrain placements appeared particularly effective in eliciting sustained thumping, and on one occasion, an animal (28D) stimulated within this area thumped 71 times in 20 minutes following stimulation. However, most sites produced only a few thumps after termination of stimulation. Three sites produced reliable thumping during stimulation. These electrodes were found at the base of the lateral ventricle, in the commissure of the fornix, and in the midline thalamus.

The emission of thumping overtime is plotted in Figure 2 for the first five trials for each of four placements within midbrain structures. The data for rabbit 28D is restricted to the first 50 responses. While it is possible that there was some decrease in the vigour or amplitude of individual thumps as emission continued, there was no obvious decrement, and the final thumps of a trial appeared as clearly recognizable as the first few. However, the interval between successive thumps steadily increased, producing an orderly decay of emission of thumping with time. Further trials produced curves essentially the same as those of the first five trials, and are omitted. The two additional sets of curves plotted in Figure 2 are those for the emission of thumps after peripheral shock for the two animals(Rabbits A & Z) that produced the greatest number of thumps in the peripheral shock experiment. These curves are similar to those of thumping after central stimulation.

REINFORCEMENT TESTING

As noted previously, stimulation at sites eliciting thumping also produced behaviours such as searching and escape. This suggested that the stimulation might have motivating properties. Since information concerning motivating properties would be of value in determining the function of thumping, reinforcement testing of points producing thumping was carried out. The procedure developed by Valenstein and Meyers(18) was used. This consisted of allowing the animal choice of side in a two-platform box in which central stimulation was delivered only on one side of the box. The positive side was switched randomly. The reinforcing value of stimulation was measured as the percentage of total time spent by the animal on the positive side.

Animals and Procedure

The two-platform box used measured 40 x 20 inches and was 14 inches high. It was open at the top. The compartments were divided in two by a bar 2 1/2 inches high, which prevented straddling of the platforms. Current was delivered to the animal by the same leads and stimulator used earlier. The box and stimulator were controlled through two Hunter timers and operant apparatus. Total stimulation time was recorded on a running time meter, and number of approaches to stimulation were recorded on a counter. Since it was noted that vigorous thumps by the animal on the side where stimulation was off would jar the microswitch on the opposite side to trigger spurious counts, the pulse which would trigger the counter for an approach to stimulation was first delayed by 1.5 seconds by a timer. It was then gated through a relay, which would only transmit the pulse if the animal had previously moved to the other side and stimulation had gone on.

Nine animals with electrodes for which the thump threshold had been determined were selected. The rabbit was placed for 60 seconds on the side where stimulation would first begin, with stimulation off on both sides. Stimulation was then delivered to the animal as previously described. The random schedule used was programmed in 20 one-minute steps, modified to ensure that stimulation switched after the first step, and the stimulation did not remain on the same side for longer than two minutes. The only cue correlated with a change of side of stimulation was the stepper click, which also occured when stimulation did not change sides. A change of side by the rabbit to initiate stimulation was followed by a counter click. After a test session, rabbits were removed from the apparatus and retests were given after a minimum interval of 24 hours.

On the initial session stimulation parameters were set at the threshold determined for thumping, and stimulation modulated in trains of 0.5 seconds on, 1.0 seconds off. This session served to train the rabbit and the data obtained were not used in subsequent analysis. Further sessions were given with this stimulus train setting, starting at threshold, and increasing the voltage by 0.5 times threshold every two sessions, up to a maximum of three times threshold voltage. This was followed by two extinction sessions if the stimulation appeared to have had an effect on the animal's behaviour. A series of trials using continuous stimulation was next carried out, starting at 0.5 times threshold voltage, to a maximum of three times threshold. Testing was discontinued before the maximum setting was reached whenever severe motor patterns were elicited or whenever the animal's behaviour with respect to the stimulus could be clearly categorized as an approach or escape-avoidance response.

During testing it was observed that a number of rabbits made very frequent approaches to stimulation. In order to test the possibility that this result was due to increased activity produced by the stimulation, bar-pressing tests were carried out. A long hook about one inch in width was constructed and fastened to a microswitch, to hang down at about chin level of a standing rabbit. Stimulation was delivered as long as the rabbit held the hook down.

Results

The percentage of time spent on the positive platform and number of approaches to stimulation are plotted in Figure 3 for eight rabbits. A ninth animal developed a superstitious response of escaping only to one side. Its responses could not be compared with the others quantitatively and the details of its performance are omitted. All nine rabbits showed a clear tendency to limit the amount of stimulation received, on at least one of the two stimulus train variables. The sites stimulated can therefore be classified as having negative reinforcing properties. At the same time five of the animals (27A, 21B, 26B, 30D, and the omitted animal) would turn stimulation on and off, a behaviour labeled "ambivalent". It therefore appears that motivational properties associated with sites eliciting thumping are either purely negative, or negative and ambivalent. The results also indicate that these motivational properties increase in strength with increases in voltage, and first begin to produce a measureable effect on behaviour, in most cases, near the threshold for thumping. In fact, thumping was frequently observed during testing. These results, however, do not necessarily suggest a one-to-one relationship between thumping and negative reinforcement. Rabbit 21B, which was originally classified as marginally reliable, was later re-classified as unreliable, when thumping could not be elicited on re-test. This point produced negative, ambivalent responding.

Of the four reliable thumping placements showing pure negative reinforcement, two were found in the central grey, one in the hippocampus-fimbria region, and one in the commissure of the fornix. Of the four placements which produced reliable thumping and ambivalence, one was found in each of the following locations: midline thalamus, diagonal band of Broca, perifornical region of the hypothalamus, and reticular formation. The unreliable placement was in the rostral thalamus in the stria terminalis-nucleus parataenialis area. The points tested varied considerably in thresholds for thumping, and in number of thumps elicited.

The preceding discussion assumes that ambivalent behaviour is an indication of an underlying motivational state. Instead, it is possible that this behaviour is increased general activity of the rabbit produced by the brain stimulation, which, although without reinforcing properties, results in a large number of crossings to the positive side of the box. This hypothesis, however, does not explain why the stimulation-produced arousal should also result in a low total amount of stimulation, since stimulation occurs equally often on both sides. A further argument against such an arousal interpretation is that two of these animals learned to press a bar to turn stimulation on and off, unequivocally demonstrating reinforcement on a complex task. Observations of the animals while responding in the two-platform box also fails to support an arousal hypothesis. A stimulation-produced increase in activity would be expected to result in random activity. However, an "ambivalent" rabbit would show little movement while on the negative platform. At intervals, ranging from a few seconds to minutes it would abruptly hop over the dividing bar and turn stimulation on. Within a few seconds after the stimulus-on response was made, and in some cases immediately, the rabbit would escape to the off side. At high voltages, interfering motor responses would frequently make these escape responses awkward, but very short escape latencies were still seen. Once escape was initiated, the response was completed very rapidly, and after escaping, the animal would remain relatively still before again responding to turn stimulation on. Thumping was frequently noted during this resting period. When the stepper initiated stimulation, the animal would immediately escape to the off side. The behaviour always appeared goal-directed with respect to the stimulus, never random.

PERIPHERAL ELICITATION OF THUMPING

The use of peripheral shock to elicit thumping was suggested both by naturalistic observations of thumping (referred to in the introduction) which usually noted thumping occuring in aversive situations, and by the results of the previous test, which correlated negative reinforcement with central elici tation of thumping. Preliminary testing confirmed that thumping could be elicited by peripheral shock. The following experiment was designed to demonstrate this in a formal experiment, and at the same time to attempt to show that thumping could be conditioned to a fear-producing situation.

Animals and Procedure

Five male rabbits were prepared, each with two shock electrodes inserted under the skin at the back of the neck. The leads were attached to insulated contacts fixed to the skull with screws and cement. The electrodes were placed in contact with both skin and muscle, on either side of the midline. Each animal was given preliminary shocks to ensure that the electrodes were effective in producing aversiveness. A discrimination procedure was used, with each rabbit always receiving shocks in one distinctive box, and never in another box. Shock was produced by a Harvard inductorium powered by two flashlight batteries.

A trial consisted of exposing the animal to both boxes. The shock leads were connected and the animal was placed in either the non-shock or the shock box (in randomized order) for 4 minutes then replaced in its cage for 15 minutes. After this interval, leads were again connected and the rabbit was placed in the other box for 4 minutes. It was then again removed to its cage. A brief shock of 0.3 seconds duration was given three times at 1 second intervals, after the rabbit was placed in the shock box.

Two trials were given each day, separated by approximately four hours, for 10 trials. The procedure was then modified in an attempt to make acquisition more efficient. Shock intensity was raised, the rabbits were removed from each box after 1 minute (i.e. immediately after receiving shock in the shock box), and trials were given at 15 minute intervals. Thirty more trials were then carried out.

Results

Thumping usually began within a few seconds after shock, and did not appear to differ from thumping elicited centrally. Responses to shock also included strong attempts to escape, very abrupt convulsive crouching, squealing, and urination. The last two responses were never elicited by central stimulation. The median number of thumps after shock was 4, with a range from 0 to 18. This compares with a median of 4 and a range of 0 to 71 for a comparable series of trials using central stimulation. The pattern of emission of thumps for the first five trials for two animals (Rabbits A and Z) showing sustained thumping is plotted in Figure 2.

The results demonstrate that thumping may be elicited by peripheral shock. However, it has not been clearly shown that thumping may be conditioned to neutral stimuli associated with the shock. Thumps were emitted in both the shock and the non-shock box in the absence of shock, but only one animal (Rabbit A) consistently emitted more thumps in the shock box than in the non-shock box. Differential responding occurred from the eighteenth trial on to the end of training. Also, frequent thumping in the home cages was now noted although this had been only rarely observed in thepast. Therefore, the observed changes in behaviour may have been a result of sensitization rather than true conditioning.

DISCUSSION

The results of this study strongly suggest that thumping behaviour in the rabbit is a fear or pain response. This conclusion is clearly supported by demonstration that thumping may be reliably elicited by peripheral shock, along with the more familiar fear responses of squealing, crouching, escape, and urination. The finding that thumping may be conditioned to occur in the test box associated with aversive stimulation is further evidence that the behaviour may be elicited in fear-producing situations. Unfortunately, it is possible to attribute this result to sensitization rather than true conditioning, since only one rabbit responded differentially in the shock and non-shock test boxes. Alternatively, the observed non-specificity of thumping may be due to the difficulty of the discrimination task for highly-aroused subjects.

Other evidence supporting the hypothesis that thumping may function as a fear response comes from the central stimulation experiments. It was found that thumping behaviour may be reliably elicited through electrical stimulation of specific areas of the rabbit brain, particularly the midline thalamus, hypothalamus and central grey. Thumping was not elicited from the cortex, corpus callosum, anterior commissure, striatum or internal capsule. The former areas correspond to those from which defensive behaviours have been elicited by stimulation in other species (7, 9, 10). It also appears that the pattern of points eliciting thumping approximates to some extent the distribution of negative reinforcing sites as mapped in the brain of the rat (16) and rabbit (3). Direct evidence of this correspondence is provided by the result that all reliable thumping points tested for reinforcing properties were found to be associated with negative reinforcement. This correlation suggests a relationship between thumping and aversiveness. Such a relationship would be expected if thumping functions as a fear response.

It appears likely that sites eliciting thumping are closely associated with the central representation of pain. In particular, the central grey and reticular formation have been shown to contain fibers which respond to noxious stimulation (14), and to produce pain-like responses on stimulation (5). These areas produced reliable thumping in the present study. In addition, there is strong evidence that the intralaminar nuclei contain terminations of the spinothalamic system responding to noxious stimulation (2, 12, 14). These nuclei closely border the midline thalamic areas where reliable thumping points were found.

However the thumping produced by central stimulation isprobably not simply a response to pain. Squealing and urination were never seen in association with such behaviour although they were regularly elicited by peripheral shock. It may be that there is a central system controlling thumping behaviour which can be excited directly by an electrical stimulus but which also receives pain afferents. The fact that similar decay curves (see Figure 2) are produced following both peripheral shock and central stimulation supports the hypothesis that a single system is involved.

A complicating factor is introduced by the finding that a number of sites eliciting reliable thumping were associated with ambivalence as well as negative reinforcement. This suggests that thumping may not occur exclusively in aversive situations. In the gerbil(11), "footstomping" has been reported to occur both after foot-shock and during sexual activity. However, the response may have different functions in the two species. Since thumping has not been observed during sexual activity (or any other appetitive behaviour) in the rabbit(14), an explanation along these lines is speculative.

In addition to functional considerations, the results presented here indicate that centrally-elicited thumping has a number of distinct properties. Particularly interesting is the observation that thumping occurs in almost all cases only after termination of stimulation. Why this should be characteristic of thumping is not known. The small number of other behaviours which have been reported at offset of an eliciting stimulus, such as penile erection in the monkey(13) and shaking in the rat(8), do not appear to possess any properties in common with thumping or with each other. At the same time it is clear that the neurophysiological mechanism mediating these behaviours must be very different from that producing the more usual stimulus-bound pattern of elicited behaviour. In the case of thumping, this hypothetical mechanism may be organized in an anterior-posterior direction, since there is some evidence that midbrain sites are more effective than diencephalic ones in eliciting sustained trains of thumping. It also appears that close regulation of emission of thumps takes place. The curves of Figure 3 generally show a smooth decay of responding over time, for both peripherally and centrally elicited thumping. The anatomical basis of a mechanism having these properties is unknown. However, it seems likely that a number of methods, such as lesion and drug procedures, as well as continuation of the stimulation techniques outlined here, may be able to elucidate these aspects of the behaviour in greater detail in future.

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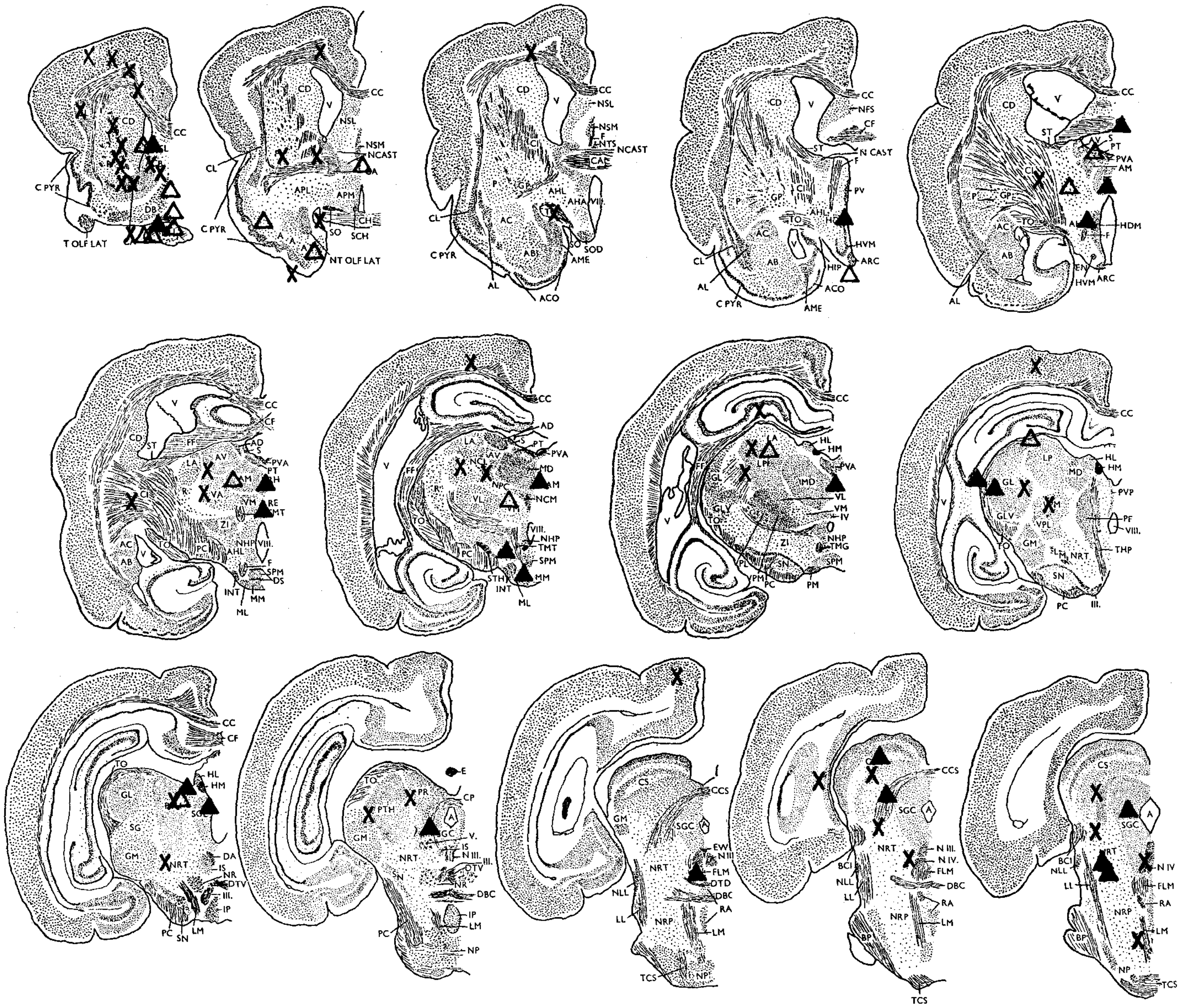
Fig. 1. Distribution of points in the rabbit brain which produce thumping behaviour when stimulated. △ , reliably elicited thumping; △, unreliably elicited thumping; ╳ , other behaviour.



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BP
CS
N IV

Fig. 2 Temporal distribution of a train of thumps following an eliciting stimulus in six rabbits. Rabbits 28D, 16E, 30D, and 20D, thumping following central stimulation; rabbits A and Z, thumping following peripheral shock. First five elicitations trials shown for each rabbit. X, trial 1; O, trial 2; △, trial 3; ●, trial 4; ▲, trial 5.

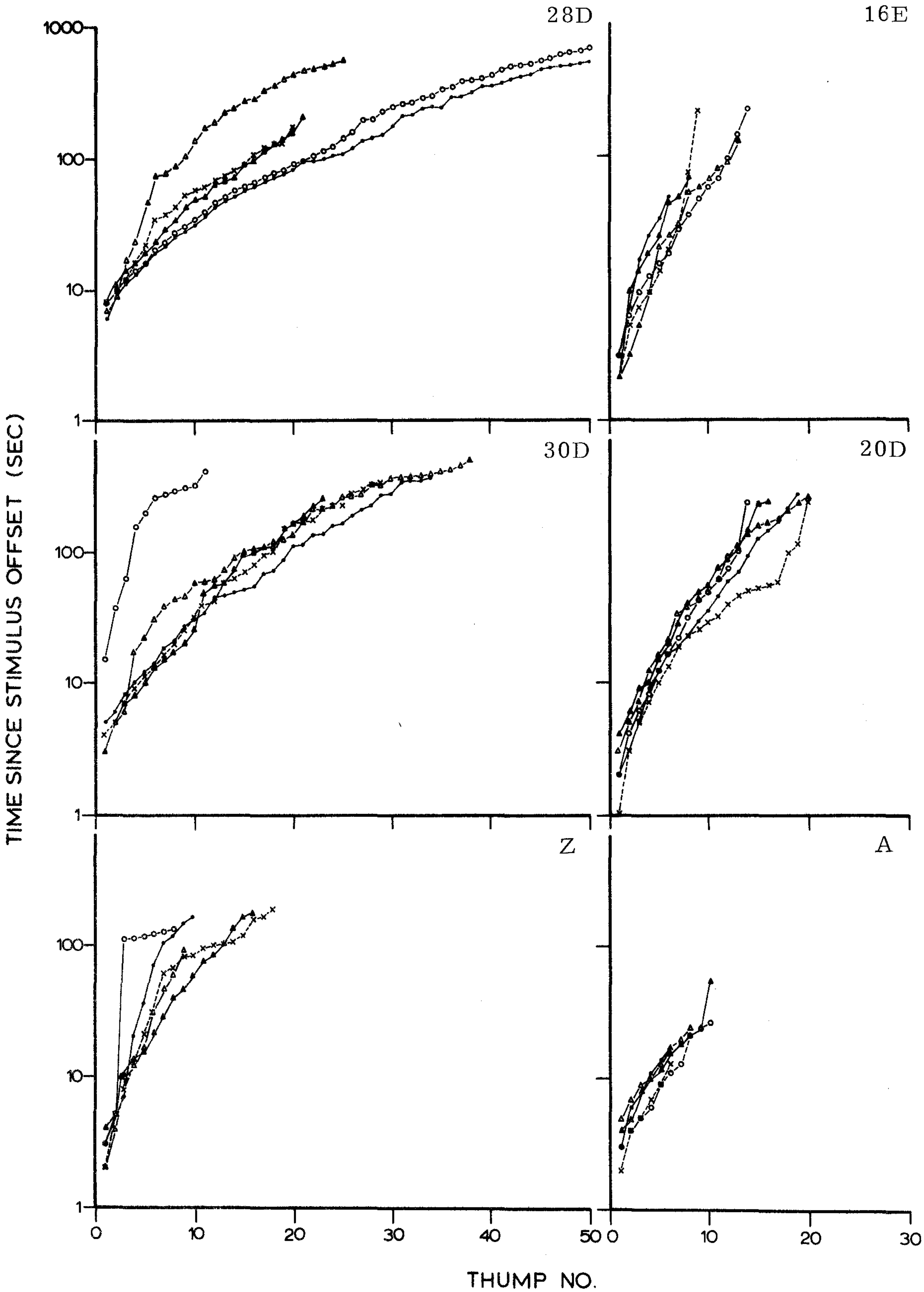
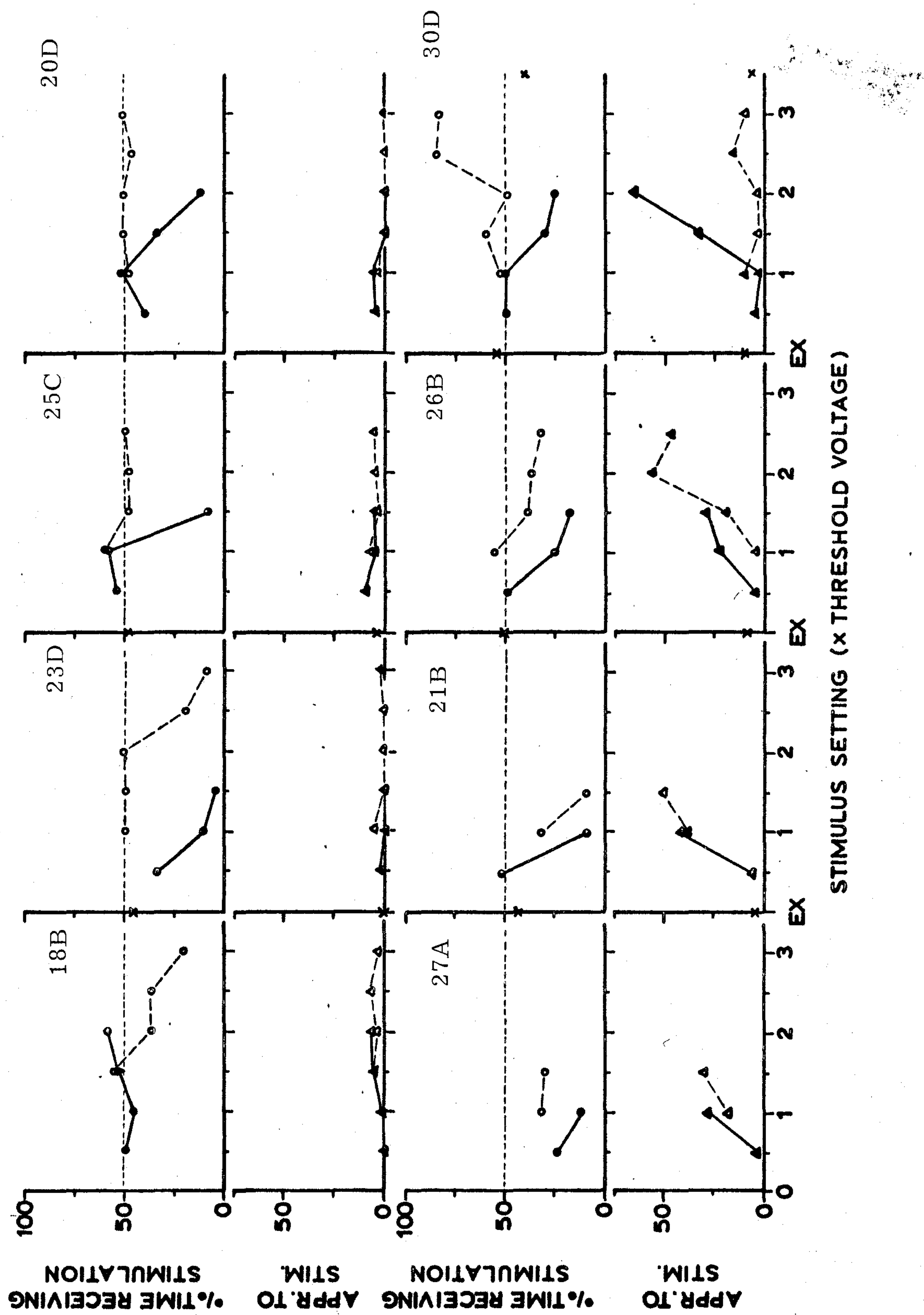

28D
16E
30D
20D
Z
A
1000
100
10
1
TIME SINCE STIMULUS OFFSET (SEC)
0
10
20
30
40
50
THUMP NO.

Fig. 3. Approaches to stimulation and time receving stimulation in self-stimulation tests in eight rabbits. Values on abscissae represent mean of two test sessions. Dotted lines, pulsed stimulation; solid lines, continuous stimulation. Ex, extinction (no stimulation).


18B
23D
25C
20D
27A
21B
26B
30D
%TIME RECEIVING STIMULATION
APPR. TO STIM.
STIMULUS SETTING (x THRESHOLD VOLTAGE)
EX