ly discriminate chemical stimuli with information contained in spike trains shorter than 1 second, such as those following individual flicks. Repetitive flicking could therefore provide multiple points for discriminating gradual odor changes. The increased flicking rates accompanying initial detection of a novel odorant would further the lobster's temporal resolution of its odor environment.

Olfaction usually affects behavior at a great enough distance from the source of an odor that the initial onset and subsequent changes in odor concentration are likely to be gradual and haphazard rather than continuously incrementing, like the changes studied here. Flicking in near-threshold, gradually changing stimulus conditions elicits phasic bursts of spikes in otherwise silent receptors (Fig. 1, first several flicks of the upper trace). The resulting ability to better detect near-threshold changes in stimulus concentration may account for the spontaneity of flicking in the unstimulated animal.

The finding that flicking temporally enhances the detection of, and emphasizes any change in, the lobster's chemical milieu is in harmony with the hypothesis (*23*) that chemical cues are the weakest of the stimulus modalities in the temporal and spatial domain. We propose that flicking represents a physiological mechanism in the lobster to compensate for the inherent temporal weakness of olfactory stimuli. Since all organisms must deal with this characteristic of olfactory stimuli, it is likely that the responses of primary chemoreceptors in the diverse organisms exhibiting phasic stimulus-receptor interaction (such as sniffing and tongue flicking) are similarly modulated in time.

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18. Spectrophotometric measurements of the amount of tryptophan loaded by five antennules in a total of 15 flick-no-flick-flick sequences varied significantly between flicked and nonflicked trials determined by a two-way analysis of variance ($P < .001$) and a posteriori testing of the means (sum of squares simultaneous test procedure, $P < .001$) (*19*).
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Feeding and Behavioral Activation in Infant Rats

Abstract. *Three-day-old rats that were separated from their mothers and deprived of food were found to be capable of feeding either from small puddles of milk or when milk was infused into the front of their mouths. Such feeding was accompanied by a dramatic increase in behavioral activity and only occurred in a warm environment. These data demonstrate that neural systems for ingestive behavior are present at birth and suggest the existence of feeding-related arousal or motivational systems.*

It has usually been assumed that neonatal rats are not able to feed in any way other than by suckling from the mother. Spontaneous eating and drinking has only been observed in rat pups starting at about 15 days of age (*1*), the beginning of the weaning period (*2*). The infant rat is notoriously resistant to being hand-fed or coaxed to suckle from an artificial nipple (*3*). The ability to recognize and ingest food has not appeared to mature until late in development and has often been presumed to arise from the suckling behaviors of infancy. I report here that even neonatal rats can feed independently of the mother, and that such feeding is accompanied by considerable behavioral activation. Both the feeding and the activation depend on temperature and deprivation conditions.

The altricial status of the newborn rat makes it, in general, an ideal subject for studies of neural and behavioral development (*4*). In this study of the development of the feeding system in rats, 3-day-old rat pups were placed near a large puddle of milk in a clear plastic observation container (*5*). The container was housed inside a moist incubator maintained at 33° ± 1°C. Pups were tested after 1/2, 7, or 22 hours of food deprivation ($N = 5$) (*6*). Food deprivation is a primary determinant of adult ingestive behavior but has little effect on the suckling behavior of young pups (*7, 8*).

The pups ingested the diet. They probed the floor with their snouts and mouthed the milk. Moreover, they increased their intake with longer periods of deprivation. Pups deprived for 1/2, 7, or 22 hours consumed, respectively, 1.5, 3.0, and 5.3 percent of their body weight in a 1/2-hour test (*9*). The pups also exhibited a marked behavioral activation in conjunction with ingestion of the diet.

In order to study the pups' ingestion more closely a procedure was developed that allowed the experimenter to program a pup's exposure to food and then observe its behavior in a structured situation (*10*). A fine polyethylene cannula was installed under the tip of the tongue in the front of the pup's mouth (*11*). This intraoral cannula could be implanted rapidly, without trauma, and did not seem to interfere with mouthing and swallowing. Pups quickly habituated to its presence (*12*). When diet was infused through the cannula a pup could eat by licking and swallowing. Or, if the pup did not active-

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ly ingest, the diet spilled out of the front of its mouth.

Pups were again tested after 1/2, 7, or 22 hours of food deprivation (*6*). One-half hour before the test began, the cannulas were implanted. Immediately before the tests, the pups' bladders were voided by anogenital stroking with a soft brush, and the pups were weighed to the nearest 0.005 g. Each pup was then placed in a clear plastic observation container in a warm, moist incubator, and its cannula was attached to a lead from a syringe containing the diet. The syringe was driven by an infusion pump. The pups were permitted a 2-minute adaptation period. Then, every 2 minutes for the next 10 minutes they received a 10-second pulse of milk delivered through their intraoral cannula (*13*). The pups responded by licking and swallowing the diet or by allowing it to spill out. Every 30 seconds throughout the test, each pup's activity was rated and various behaviors were scored on a checklist (*14*). At the end of the test, the pups were reweighed and milk intake (weight gain) was expressed as a percentage of the total amount of infused diet.

When injections were made into the front of their mouths, the pups consumed the diet and increased their food intake as deprivation was increased (*15*) (Fig. 1a). Pups deprived for 22 hours consumed 78 percent of the infused diet or about 2 percent of their body weight. During the test, the pups made mouthing movements which consisted of frequent jaw opening and closing and tongue protrusion. They also probed and mouthed the surface in front of them. This behavior, which resembles feeding of the adult rat in that increased deprivation stimulates increased consummatory activity and food intake (*16*), differs from the stereotypic extensor reflex that pups utilize during suckling (*8*) and thus distinguishes this ingestion from that of suckling.

The tests with the programmed diet delivery also revealed that the feeding and mouthing responses of pups deprived of food for 22 hours did not occur in isolation but were accompanied by dramatic behavioral activation (Fig. 1b). During the adaptation period (the first 2 minutes of the test) 22-hour deprived pups were slightly more active than pups deprived for 1/2 hour or 7 hours, but the first injection of diet produced a profound increase in activity in the 22-hour-deprived pups. These pups remained highly active (*17*) even during the time when diet was not infused.

Throughout the period of heightened activity the deprived pups displayed a variety of behaviors, among which head probing and rolling over were dominant. The head probing along the floor and into corners of the test container was usually associated with mouthing and locomotion (Fig. 2b). These behaviors often resembled adult feeding behavior. When pups rolled over they also often extended their heads and reached into the air or against a wall of the container (Fig. 2c); this behavior resembled the nipple search behavior displayed by pups when a mother settles down over them to nurse. Other behavior patterns in the pups resembled adult behavior patterns and postures, such as face-grooming and anogenital or hind-paw licking. Repeated

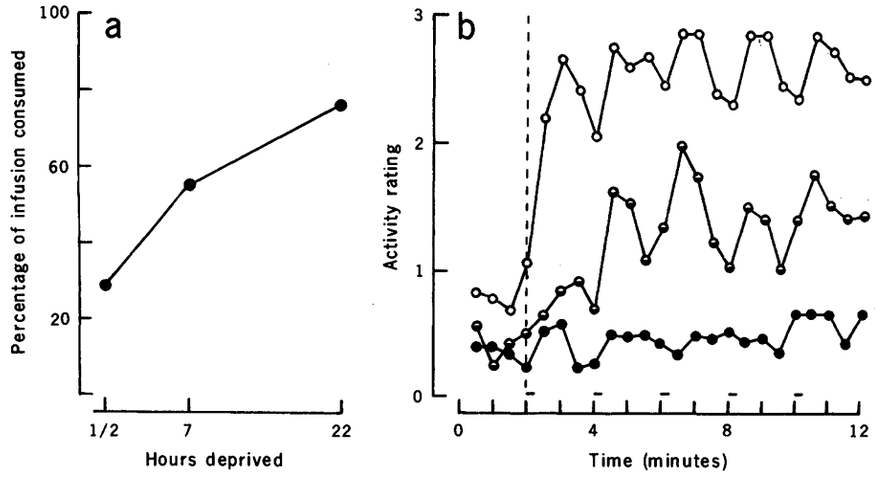

Fig. 1. (a) Mean percentage of the infused diet consumed by 3-day-old pups deprived 1/2, 7, and 22 hours (N = 5). (b) Mean activity scores by 30-second intervals for 3-day-old pups. Filled circles, pups deprived for 1/2 hour; half-filled circles, 7 hours; open circles, 22 hours (N = 5). The first 2 minutes of the test were an adaptation period; no milk injections were made. At 2 minutes and at each 2 minutes thereafter (indicated by the horizontal bars), a 10-second infusion of diet was made. Pups were rated on the basis of the highest activity they obtained in the 30-second interval (*14*).

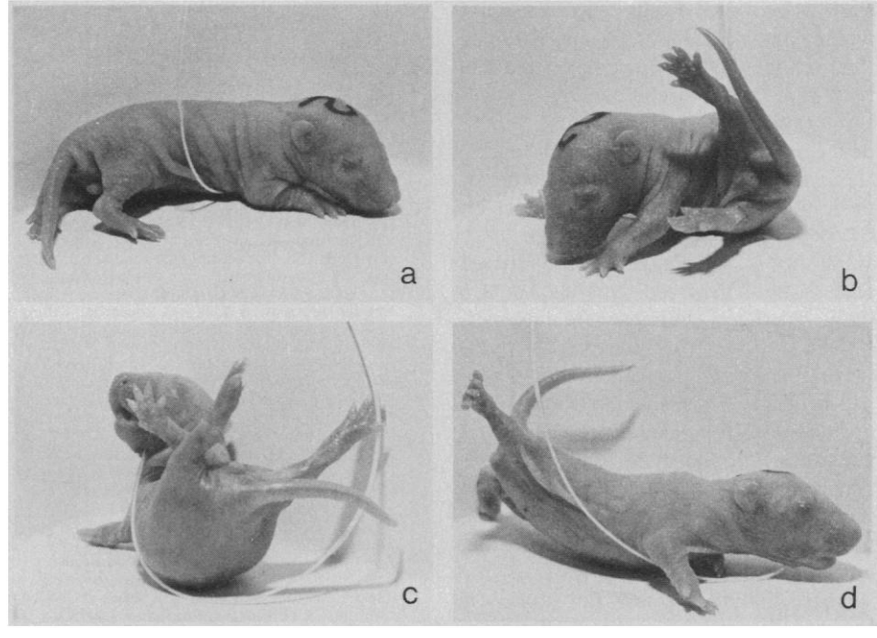

Fig. 2. The effects of diet infusions on the behavior of a 3-day-old pup deprived for 22 hours. In (a), the pup is quiet and relaxed; an infusion has not yet been made. The intraoral cannula is shown emerging from under the pup. At the start of the infusion, the pup immediately begins to probe the floor with its snout. The probing becomes more vigorous, and the pup seems to lose control of its body (b). During the probing, pups usually make mouthing and licking movements; more general body movements follow. These include curling and pelvic thrusting (c), stretching, kicking, and tail-flailing (d), and locomotion and probing about the cage. Pups show these behaviors both during and after infusion. Depending on how recently they have tasted the diet, pups also show these behaviors, although somewhat erratically, when they are feeding from puddles of milk. The infusion procedure allows a more careful and controlled analysis of this behavioral activation in response to diet.

extension (Fig. 2d) and curling of the trunk occurred during periods of activity, and occasional thrusting with the hindquarters was observed (*18*). The level of activity during these tests was particularly impressive because the infant rat usually exhibits little spontaneous locomotion. Such activity reflects more than a general hyperreactive state of deprived animals because strong tactile stimulation did not produce similar behaviors or activation.

The extent of the feeding and the behavioral activation in the rat pups depended on both the severity of the food deprivation (*19*) and the temperature of the environment. When pups were tested at room temperature (24°C) and compared to pups tested in an incubator, those at room temperature neither ate as much (31.2 percent of the infusion consumed as opposed to 68.3 percent, $N = 9$) nor became as active (9.9 percent total activity compared to 24.3 percent) as those at 33°C. The decreased response at room temperature was not due to debilitation by the cold, because pups tested at room temperature were removed from the incubator only moments before they were tested (*20*). In fact, activity scores for the 2-minute adaptation period were higher for the pups tested at room temperature. Yet these pups reacted aversely to diet injections, frequently waving their heads in the air, scraping their chins on the floor, and treading backward (*21*) before becoming relatively motionless. This temperature dependence may reflect a state of "well-being" (*22*), normally provided by the mother or nest, which has a permissive effect on the pups' perception and behavior.

Parallel experiments were conducted with 22-hour deprived pups aged 1 to 6 days. The 6-day-old pups were more persistent than the 3-day-old pups in probing and licking the floor, but they still engaged in a variety of behaviors. After 6 days of age, the generalized behavioral activation produced by diet infusions disappeared. It was replaced by directed ingestive responses in which the pup engaged in concentrated mouthing, licking, and lapping focused in one spot.

These findings demonstrate that portions of the neural mechanisms for feeding behavior are present at birth in rats even though the pups may never use them (*23*). The feeding observed in these experiments has probably not been observed previously because of the special conditions required: severe food deprivation and warmth. Such deprivation would be unlikely to occur naturally (*24*). Nonetheless, these experiments reveal the existence of a feeding mechanism in rats that can be studied from birth (*25*). The data also reveal that the neonatal rat can be behaviorally activated by food. This activation is not restricted to motor responses of the feeding system but in young pups seems to extend to the pup's whole body and to other behaviors. Such behavioral activation may be related to developing neural arousal and reward systems associated with consummatory behaviors and may prove useful in studying the development and organization of motivational systems.

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3. The rat differs from many other animals that, as neonates, can easily be hand-fed.
4. The suitability of the rat pup for these types of studies has been emphasized by J. T. Kenny and E. M. Blass [*Science* **196**, 898 (1977)], J. W. Rudy and M. D. Cheatle [*ibid.* **198**, 845 (1977)], and L. F. Lanier, A. J. Dunn, and C. Van Hartesveldt [in *Reviews of Neuroscience*, S. Ehrenpreis and I. J. Kopin, Eds. (Raven, New York, 1976), vol. 2, p. 195].
5. The plastic container was 12 cm in diameter; the milk used as the test diet in these experiments was commercially available "half and half" (half milk, half cream), in which the amounts of water and fat are similar to rat milk.
6. Deprivation took place in a humidified incubator (33° ± 1°C) that maintained the pups' axillary temperatures at 35° to 37°C, the same range as in the home nest. Pups were placed in groups in small containers on fresh bedding. They were thus deprived of food and water as well as suckling and maternal care. Only one pup from a litter was used in each condition.
7. Similar deprivation does not affect the willingness of young pups to initiate suckling [W. G. Hall, E. M. Blass, C. P. Cramer, *J. Comp. Physiol. Psychol.* **91**, 1141 (1977)] or the volume of milk consumed during certain suckling tests (*8*), though deprivation can influence the amount of milk obtained in the natural suckling situation [K. A. Houpt and A. N. Epstein, *Am. J. Physiol.* **225**, 58 (1973); K. A. Houpt and T. R. Houpt, *J. Comp. Physiol. Psychol.* **88**, 764 (1975); M. I. Friedman, *ibid.* **89**, 636 (1975)].
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9. As in the following experiment, food intake was determined by weighing pups (to the nearest 0.005 g) before and after the tests. Increased food intake with deprivation was significant, F (2, 12) = 8.49, $P < .01$. Mean absolute intakes were 0.13, 0.28, and 0.42 g. In a replication of the experiment, food intake was greater when a thin towel soaked with diet was placed on the floor of the test container. This method distributed the diet evenly and helped the pup to avoid getting diet up its nares when probing into a puddle.
10. The procedures used here were developed from a technique that was devised to study drinking [J. Wirth and A. N. Epstein, *Am. J. Physiol.* **230**, 188 (1976)]. These authors obtained licking and swallowing responses in young pups held at a flowing water spout. Limited licking and swallowing in response to oral stimulation have also been reported by C. R. Almli and R. S. Fisher [*Brain Res. Bull.* **2**, 425 (1977)].
11. Cannulas were constructed from an 8-cm piece of polyethylene tubing (PE-10, Clay Adams). A small flange (1.6 mm in diameter) was formed at the tip by heating the end of the tubing until it blistered, then pressing it flat on a smooth surface. Cannulas were installed by friction fitting the nonflanged end of a cannula over a piece of curved music wire (0.255 mm in diameter), and then inserting the wire into the pup's mouth and down through the soft part of the jaw behind the roots of what would become the lower incisors. The cannula flange was then pulled flat against the inside of the jaw.
12. Pups with a similar cannula will attach to their mothers' nipples and suckle soon after it has been installed (*8*).
13. The pump was adjusted so that the total infusion volume of five injections would equal 2.5 percent of the average body weight of pups of a particular age. For 3-day-old pups, a total of 0.28 ml was injected. These infusion rates are slightly faster than the pups can swallow, to help preclude a ceiling effect. Delivering diet in this pulsed fashion permitted observation of pups during feeding and during intervals when food was not infused.
14. Trained observers made activity ratings by using the following scale, with 0.5 interval between points: 0, no movement; 1, head or slight forelimb movement; 2, locomotion; 3, vigorous locomotion. We have had experience with this rating system, and interobserver correlations are about 0.85. Pups were also scored for the occurrence of mouthing, probing, rooting along the floor or into corners, rolling over, and various body movements such as curling, head waving, and treading. These data will be reported in detail (W. G. Hall, *J. Comp. Physiol. Psychol.*, in press).
15. Increased deprivation produced a significant increase in intake, F (2, 12) = 9.88, $P < .005$.
16. The ingestive behavior of these young rats is not, however, identical to adult feeding, and some of the behavioral changes during later development are noted below. Nonetheless, there is sufficient resemblance that I think the terminology is appropriate. Feeding in the 3-day-old pup is more than just reflex swallowing. Swallowing does not seem to be affected by deprivation, because when diet was injected through cannulas placed in the back of the mouth (*8*), intake was similar at all deprivations (76 to 89 percent).
17. Total activity differences between groups for the 10-minute feeding period were significant, F (2, 12) = 14.43, $P < .001$. In testing extended beyond 15 minutes, the pups' activity decreased. This decrease occurred after the pups had ingested a large volume of milk, and it could also be produced with stomach loads of milk.
18. With unusual types of stimulation, movement patterns can be elicited in advance of their normal development [C. Gard, E. Hård, K. Larsson, V. Petersson, *Anim. Behav.* **15**, 563 (1967)]; H. Szechtman (paper presented at Eastern Psychological Association meeting, Boston, Mass., 1977) has shown that mild tail pinch of a 3-day-old rat will induce licking and probing much like tail pinch induces eating in the adult rat.
19. While pups were maternally deprived as well, it seems unlikely that this was a primary stimulus for the feeding or activation since these behaviors were depressed with the accumulation of milk in the stomach (*17*).
20. Difference in intake, t (8) = 9.65, $P < .001$; difference in activity, t (8) = 10.78, $P < .001$. Body temperature differences were not greater than 1.5°C at the start of infusions, though they increased by the end of the test. However, when pups cooled to axillary temperatures of 29°C were placed in the incubator and immediately tested, they responded with activation and intake. Temperature of infused diet was not critical to any of the effects.
21. These behaviors are observed in adult rats when they are eating a distasteful food or a food previously associated with poisoning.
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23. The finding that infant rats will feed when milk is infused into the front of their mouths is in accord with suggestions from electrophysiological and lesion data that lateral hypothalamic substrates of feeding are at least partially mature in the infant rat [C. R. Almli, N. T. McMullen, G. T. Golden, *Brain Res. Bull.* **1**, 543 (1976); C. R. Almli and G. T. Golden, *J. Comp. Physiol. Psychol.* **90**, 1063 (1976)]. These systems may not even be required for all the pup's responses since both decerebrate adult rats and neonatal rats are capable of ingestive responding [H. J.

Grill and R. Norgren, *Science* **201**, 267 (1978); *Brain Res.* **143**, 281 (1978); C. Kornblith and W. G. Hall, *J. Comp. Physiol. Psychol.*, in press].
24. Even if the young pup normally exhibited this independent type of ingestive behavior, it is unlikely that it would have survival value since any liquid food available to the pup is unlikely to be nutritionally adequate.
25. Feeding can be analyzed in pups which have had no feeding experience other than suckling. Suckling experience is not required for the normal appearance of feeding [W. G. Hall, *Science* **190**, 1313 (1975)]. This report represents one of several demonstrations of the independence of systems underlying suckling and feeding (*7, 8*).
26. I am grateful to T. Bryan for assistance; to E. M. Blass, S. Coyle, C. Kornblith, R. W. Oppenheim, J. S. Rosenblatt, and C. L. Williams for comments on an earlier version of the manuscript; and to A. E. Johnson for photography. Supported by NSF grant BNS 77 23051 and the North Carolina Division of Mental Health.

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Medial Septal Lesions Retard Classical Conditioning of the Nictitating Membrane Response in Rabbits

Abstract. *Lesions of the medial septum were produced in 7 of 14 rabbits prior to classical conditioning of the nictitating membrane response. Lesions significantly altered the hippocampal electroencephalogram, attenuated conditioned hippocampal unit responses, and slowed the behavioral rate of acquisition. The contrast of the behavioral results with those of studies of massive septal or hippocampal ablation suggests a functional subdivision of the septo-hippocampal system in learning.*

The hippocampal formation of the mammalian forebrain is thought to be involved in processes central to learning and memory (*1*). It has been suggested that disrupting the hippocampal electroencephalogram (EEG), especially the highly synchronous theta rhythm, with electrical stimulation (*2, 3*), drugs affecting central cholinergic mechanisms (*4*), or lesions of the medial septal nucleus (MSN) (*5, 6*) impairs the learning of a variety of tasks. Interpretations have implicated both acquisition and retention and have questioned whether impairment is restricted to specific tasks (for example, spatial or cue learning) (*5, 6*), or involves more general processes (for example, learning, consolidation, attention, or arousal) (*2, 4*).

We have recently reported evidence of a strong relationship among frequencies in the hippocampal EEG, learning-related changes in hippocampal neuronal activity, and differences in acquisition rate of the classically conditioned nictitating membrane (NM) response in rabbits (*7*). We have also demonstrated that subareas of the septal region show changes in activity related to different aspects of this conditioning paradigm (*8*). The MSN response can best be interpreted as one of arousal in that MSN units show brief, stimulus-evoked responses that decrease with repeated stimulus presentations (*8*). In contrast, units of the lateral septal nucleus, like those of the hippocampus, show learning-dependent plasticity—that is, marked increases in activity that model the amplitude-time course of the conditioned NM response (*9*).

In the light of this evidence, it is surprising that massive ablations of either hippocampus or septum have little effect on acquisition or retention of the NM response in rabbits (*10*). Abnormal activity may be more detrimental behaviorally than removal of the hippocampus itself (*11*), an interpretation supported by studies of NM conditioning using disruptive hippocampal stimulation (*3*). Massive septal lesions not only disrupt hippocampal activity by damaging the medial septal "pacemaker" for theta, but also interrupt major subcortical hippocampal efferents through the lateral septal nucleus (*12*). It can thus be hypothesized that lesions restricted to the MSN impair NM conditioning more than large septal or hippocampal lesions, because major pathways conveying abnormal hippocampal activity would be left intact. Also, such specific disruption of the septo-hippocampal system during NM conditioning of rabbits can address questions concerning the task specificity of septo-hippocampal processes. If septal damage disrupts nonspatial learning (such as NM conditioning), arguments can be made for a septal role in learning common to both spatial and nonspatial tasks.

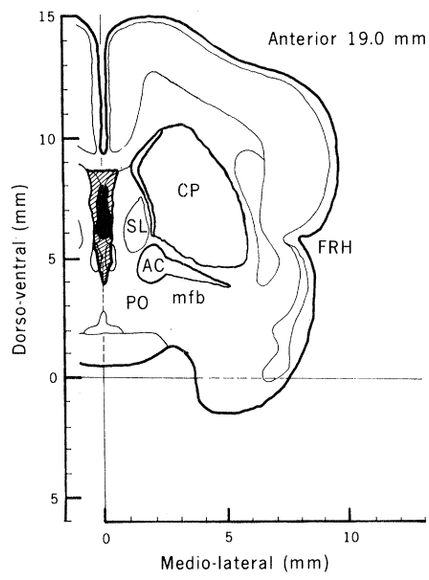

Fig. 1. Coronal section of rabbit forebrain showing the minimum (solid) and maximum (striped) extent of MSN lesions. The regions of the lateral septum and diagonal band are undamaged. Abbreviations: *AC*, anterior commissure; *CP*, caudate putamen; *FRH*, rhinal fissure; *mfb*, medial forebrain bundle; *PO*, preoptic area; and *SL*, lateral septal nucleus.

With these questions in mind, we assessed the effects of small, theta-disrupting MSN lesions on NM conditioning, hippocampal EEG, and multiple-unit activity of the CA1 area of the dorsal hippocampus. Fourteen New Zealand White rabbits (*Oryctolagus cuniculus*) had stainless steel insect pins, insulated except for 50 to 70 μm at the tip, implanted in the dorsal hippocampus for recording EEG and unit activity. All surgery was performed under halothane anesthesia, and electrodes were localized by a combination of stereotaxis and physiological recording during implantation. Skull screws and dental acrylic secured the recording electrodes to the skull. One skull screw served as a reference for recordings. Seven of the rabbits received midline septal lesions as follows. An insect pin insulated except for 200 μm at the tip, was lowered along the midline of the forebrain until the characteristic bursting pattern of MSN cells was observed. The electrode was lowered further until this bursting began to fade, at which point a d-c electrolytic lesion was made. Two additional lesions were made, 0.5 and 1.0 mm dorsal to the original lesion. Current parameters were 0.8 to 1.0 mA for 8 to 10 seconds at each placement.

Animals were given 8 to 10 days to recover from surgery and were then conditioned according to a standard paradigm (*7–9*). They were trained to a criterion of eight of nine consecutive conditioned responses (CR's) (*13*) or for a total of 4 days. Each daily session consisted of 13 blocks of trials [eight paired CS-UCS trials, and one test CS-alone trial per block (*14*)]. The CS was a 350-msec, 1-kHz, 85-dB tone and the UCS was a 100-msec corneal air puff at 210 g/cm^2, which began 250 msec after CS onset and terminated with the CS. Prior to the first conditioning trial, 2-minute EEG samples were recorded to assess the amount of theta in the spontaneous EEG. During training, multiple-unit activity from the

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