REPRODUCTIVE AND REGULATORY BEHAVIOURS IN THE FEMALE HAMSTER FOLLOWING TRANSECTIONS OF THE LATERAL CONNECTIONS OF THE MEDIAL PREOPTIC AREA-MEDIAL ANTERIOU HYPOTHALAMIC CONTINUM

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Reproductive and Regulatory Behaviours in the Female Hamster Following Transections of the Lateral Connections of the Medial Preoptic Area-Medial Anterior Hypothalamic Continuum

by

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ABSTRACT

Parasagittal knife cuts with a varied mediolateral position were placed along the medial preoptic area—medial anterior hypothalamic continuum (MPOA-MAH) in female hamsters. Near lateral (NL) knife cuts severed mediolateral connections between the MPOA-MAH and the medial forebrain bundle (MFB) while far lateral cuts (FL) were placed more laterally, sparing MPOA-MAH - MFB connections. Across the knife cut condition, hamsters were either allowed to construct and maintain a food hoard or given daily food rations. Prior to, and after surgery, animals were tested for male-soliciting ultrasonic vocalizations and maternal behaviours. Both NL and FL cuts reduced rates of ultrasonic calling. These cuts also converted into cannibals those animals which previously behaved maternally towards foster pups in preoperative virgin maternal tests. These cuts were less effective in this respect if the hamsters were allowed to hoard. These same animals were then mated and later tested for maternal behaviour with their own young. The results of the behavioural testing early in the postpartum period revealed no differences among the experimental groups in various maternal behaviours. Throughout lactation, however, the majority of NL and FL hamsters given daily food rations progressively cannibalized their entire litters. NL and FL counterparts with the hoarding opportunity, on the other hand, cannibalized fewer pups and reared healthy, moderate-sized litters that were smaller than those of appropriate surgical controls. This is the first study to demonstrate that rodents with (NL) hypothalamic cuts which ordinarily disrupt maternal behaviours, will, under appropriate testing conditions, rear litters. In view of this finding, the nature of the

maternal deficit following hypothalamic cuts is discussed. That FL cuts were just as effective as NL cuts in reducing ultrasonic calling and disrupting maternal processes suggests that mediolateral connections of the MPOA-MAH, other than with the MFB, are important for these behaviours. Possible amygdalar-hypothalamic pathways mediating these behaviours are discussed. The effects of the knife cuts and hoarding condition on body weight and other regulatory behaviours are also evaluated.

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INTRODUCTION

General Introduction

Over the years a considerable amount of experimental data has been collected in the area of rodent maternal behaviour, much of this work dealing with hormonal and neural control of this behaviour. A comparison of two recent review papers, one dealing with rat maternal behaviour (Rosenblatt, Siegel, and Mayer, 1979) and the other dealing with hamster maternal behaviour (Siegel and Rosenblatt, 1980), is testimony to the fact that the rat has been the rodent species of preference in studies of maternal behaviour. The former review is 87 pages long and the latter is 10 pages long. This difference indicates a need for more work in the area of hamster maternal behaviour. While the rat is generally the preferred laboratory animal, there are specific methodological and practical reasons for shunning the hamster in maternal research that will become evident in subsequent portions of this work.

Recently, however, the use of the golden hamster as an experimental species in behavioural research has increased. Hamsters show easily elicited and quantifiable behaviour, and are well suited for studies of mating behaviour (Malsbury, Kow, and Pfaff, 1977; Ostrowski, Scouten, and Malsbury, 1981), agonistic behaviour (Floody and Pfaff, 1977a), and behavioural rhythmicity (Zucker and Stephan, 1973). Hamsters also show behavioural patterns which contrast with that of the rat (Fleming, 1978; Payne and Swanson, 1971; Marques and Valenstein, 1976), which make them intrinsically interesting to study.

In the following sections various aspects of maternal care will be reviewed. It will be necessary to draw on studies of maternal behaviour of other rodents to fill the gaps in the hamster literature.

Description of Hamster Maternal Behaviour

Gestation in the hamster lasts 16 days. Hamsters build nest prior to gestation. However, just prior to parturition nesting activity increases and more elaborate nests are built (personal observations). Parturition occurs at the nest site, with the parturient female cleaning newborn pups of amniotic membrane. This, in addition to the umbilical cord and placenta, is ingested by the dam (personal observations; Rowell, 1960). Thereafter, postparturient hamsters display a number of nurturent behaviours which are essential for the survival of the young. Pups are kept warm, groomed, nursed, and retrieved when they stray from the nest. Beginning at mid-lactation (Day 13-15 postpartum) the frequency of these behaviours progressively declines until weaning (Rowell, 1960; 1961a). Weaning of pups is believed to occur at 24-30 days postpartum (Rowell, 1961a; Swanson and Campbell, 1980), butthere is evidence that pups begin ingesting solid food at half that age (Miceli and Malsbury, unpublished manuscript).

In addition to these nurturent behaviours, intact or otherwise experimentally untreated hamsters cannibalize portions of their litter early in the postpartum period. Early workers concluded that postpartum cannibalism reflected a breakdown in normal processes (Hindle and Magalhaes, 1957; Silvan, 1966; Summer, 1972). In a series of experiments, Day and Galef (1977) ruled out this conclusion by demonstrating that several of the assumed disruptive factors did not, in fact, influence the frequency of this behaviour. These workers maintain that postpartum cannibalism is a controlled and regulated behaviour, hamster dams cannibalizing to a "preferred" litter size. Hamster dams will behaviourally compensate for experimental alteration of litter size by cannibalizing more when foster pups are added to their own litter and cannibalizing less when pups are removed from their own litter. Recently, it has been shown that postpartum cannibalism is heavily influenced by whether or not hamsters are able to compile and maintain a hoard prior to and throughout lactation (Miceli and Malsbury, unpublished manuscript). Food hoards may be an important additional source of food for pups in mid-lactation because milk yields are believed to decrease at this point in lactation (Miceli and Malsbury, unpublished manuscript; Rowell, 1960). Postpartum cannibalism, therefore, may represent an adaptive form of regulating litter size in response to milk and solid food supply.

Hormonal Control of Maternal Behaviour

In rats, maternal behaviour is thought to have hormonal and non-hormonal bases. The hormonal changes occurring near the time of parturition are believed to be responsible for the rapid induction of maternal behaviour (Moltz, Lubin, Leon, and Numan, 1970; Terkel and Rosenblatt, 1972). After its onset, continued expression of maternal behaviour is thought to be supported by pup-related stimuli rather than by continued hormonal stimulation (Rosenblatt, 1967; 1970; Fleming and Rosenblatt, 1974c). Evidence for some aspects of rat maternal behaviour being independent of the hormonal conditions of gestation and lactation comes from the fact that virgin or non-lactating females will show maternal behaviour after 5-11 days of continuous exposure to foster young (Rosenblatt, 1967; Terkel and Rosenblatt, 1972). Induction of maternal behaviour by continuous exposure to foster young is referred to as sensitization or concaveation.

Non-pregnant rats transfused with the blood of puerperal animals will almost immediately show maternal responsiveness to foster young, but this does not occur in non-pregnant animals transfused with the blood of 24 hr postpartum animals (Terkel and Rosenblatt, 1968; 1972). This strongly suggests a hormonal, or at least, humoral, factor associated with the rapid onset of maternal behaviour in puerperal rats. The effects of gland ablations and exogenous hormone administration on maternal onset are not so dramatic (Moltz, Levin, and Leon, 1969; Moltz and Weiner, 1966). The more notable studies of hormones and maternal behaviour are those in which combinations of hormones are sequentially administered in non-lactating rats so as to mimic the hormonal dynamics of late gestation-early lactation. Administration of progesterone, estrogen and prolactin in ovariectomized virgin rats in such a sequence substantially reduced the latency to maternal behaviour (Moltz et al., 1970).

On first presentation, the naive virgin rat will show disinterest in or avoidance of foster pups (Fleming and Rosenblatt, 1974c). In the same situation, hamsters will either show spontaneous maternal behaviour or cannibalism of foster pups. In initial studies cannibalism was the predominant first response shown towards hamster pups (Richards, 1966a; 1966b). In more recent studies it has been demonstrated that up to 50% of virgin hamsters will display maternal behaviour at first contact with foster pups (Marques and Valenstein, 1976). In contrast to the rat, there is no evidence of ovarian modulation of maternal onset in the hamster. Ovariectomy had no effect on the initial response shown towards test pups (Marques and Valenstein, 1976) or on the subsequent appearance of maternal behaviour (Siegel and Rosenblatt, 1978). Similarly, the experimental manipulation of hormonal levels in pre- and postpartum hamsters had no effect on the appearance of maternal care (Siegel and Greenwald, 1975).

The hamster literature suggests that pup-related and environmental stimuli play a major role in determining the nature of the virgin's pup-directed response. Older test pups are more likely to be treated maternally than younger test pups (Noirot and Richards, 1966; Richards, 1966a). Pups are also more likely to be treated maternally if they are presented in neutral test arenas (Marques and Valenstein, 1976; Rowell, 1961) or if they are placed in the nest in the home cage situation (Rowell, 1961). Recently, it has been shown that the opportunity to hoard food can also facilitate the expression of maternal behaviour in virgin hamsters (Miceli and Malsbury, in preparation).

Neural Mechanisms

Because the limbic system is thought to underly species-typical behaviour in rodents (Carlson and Thomas, 1968; Lamb, 1975) much of the early brain research related to maternal behaviour emphasized limbic structures.

In addition to sensory functions, the olfactory system, because of its intimate anatomical relations with the limbic system, also has limbic functions. Indeed, experimental damage to the olfactory system results in dramatic changes in a number of behaviours (Doty, Carter, and Clemens, 1971; Hilger and Rowe, 1975; Leonard, 1972; Miro, Canguilhem, and Schmitt, 1980). Odors have an important modulatory function in the female rodent's response to pups (Fleming and Rosenblatt, 1974c). Consequently, considerable attention has been drawn to olfactory control of maternal behaviour. In mice, olfactory bulbectomy led both virgin and lactating mice to cannibalize pups (Gandleman, Zarrow, Denenberg, and Myers, 1971). In rats the effects of olfactory damage are more complex. While one stage bublectomy leads to either cannibalism of foster pups or a shortened latency to maternal behaviour, unilateral or two stage bilateral bulbectomy produces only the latter effect (Fleming and Rosenblatt, 1974a). Peripheral anosmia produced by either zinc sulphate nasal infusion or lesions of the lateral olfactory tract produced more consistent results. In each case anosmia resulted in an abbreviated latency for virgin rats to become maternal (Fleming and Rosenblatt, 1974b).

It has become apparent that there are two morphologically and functionally distinct olfactory systems (Raisman, 1972; Scalia and Winans, 1976); the main olfactory system and vomeronasal system, each projecting to different portions of the limbic forebrain (Cain, 1974; Scalia and Winans, 1976). In order to elucidate which system is relevant to maternal behaviour, Fleming, Vaccarino, Tombasso, and Chee (1979; with rats) and Marques (1979; with hamsters) selectively damaged the main olfactory or vomeronasal systems, or combined the procedures. In the virgin rat, damage to each system facilitated the onset of maternal behaviour; when both systems were damaged the facilitative effects were additive (Fleming et al., 1979). In virgin hamsters, vomeronasal deafferentation reduced pup cannibalism and facilitated maternal behaviour. Main olfactory system sensory loss, had no effect on hamster maternal behaviour, but when combined with vomeronasal nerve cuts, enhanced the facilitative effects of vomeronasal deafferentation (Marques, 1979). Evidently, the olfactory systems ordinarily act to inhibit the expression of maternal behaviour in virgins.

The lesion technique has been used extensively to investigate the influence of several other limbic structures on maternal behaviour. Septal lesions alter normal maternal patterns in a number of rodents. Postpartum rats sustaining septal lesions fail to nurse their young, do not build nests, and show a deficit in sequential aspects of pup retrieval (Fleischer and Slotnick, 1978). These rats repeatedly pick up and drop pups, and appear to aimlessly carry them about the cage. These workers also report that septal rats may also cannibalize if they are not given sufficient time to recover from the "septal syndrome" prior to parturition. A similar cannibalistic tendency and failure to nurse and build nests was observed in septal lesioned rabbits (Cruz and Beyer, 1972). Nesting and retrieval deficits similar to those of the rat are also reported in septal mice (Slotnick and Nigrosh, 1975) and hamsters (Goodman, Jansen, and Bunnell, 1967).

The nature of the maternal deficit in septal animals is not entirely clear. The finding that virgin rats with septal lesions do sensitize, but show the same disorganized maternal behaviours as their postpartum counterparts, suggests that it is not a motivational deficit (Fleischer and Slotnick, 1978). Interpretations of the nature of the maternal deficit following septal damage include (a) failure to inhibit inappropriate responses which interfere with ongoing maternal behaviour (Slotnick and Nigrosh, 1975) and (b) failure to sequentially integrate components of maternal behaviours into larger units (Carlson and Thomas, 1968).

Lesions of the dorsal hippocampus in the rat result in increased maternal cannibalism and deficiencies in nursing, nest building, and pup retrieval (Kimble, Rogers, and Hendrickson, 1967). Hippocampal lesions also eliminated nest building in the hamster (Shipley and Kolb, 1977). The fimbria, a collection of fibers coursing along side the hippocampal ridge, has also been lesioned and alterations in maternal behaviour observed. As with septal and hippocampal rats, fimbria lesioned rats show most components of maternal behaviour, but fail to organize them into larger meaningful units (Terlecki and Sainsbury, 1978). These rats typically build multiple nests in one observation box, and on retrieval tests do not retrieve all pups to one nest site.

Amygdaloid lesions did not produce any observable alteration in maternal behaviour of mice (Slotnick and Nigrosh, 1975). However, more recently, an inhibitory amygdaloid influence on maternal behaviour has been demonstrated. Virgin rats sustaining damage to the cortico-medial amygdaloid nucleus show a reduced latency to maternal behaviour (Fleming, Vaccarino, and Luebke, 1980).

While a considerable amount of work has gone into limbic forebrain involvement in maternal behaviour, virtually no attention has been paid to midbrain involvement. Here, the only relevant study is one in which rats received lesions of the ventral tegmental area. Rats with such lesions did not build nests or retrieve pups and most frequently cannibalized their litters (Gaffori and Le Moal, 1979). The ventral tegmental area is known to receive input from and project to the amygdala, medial preoptic area, and nucleus accumbens (Phillipson, 1979; Simon, Le Moal, and Calas, 1979); structures established as being important for maternal behaviour in rats (see above and below). Given the strong reciprocal connections between the ventral tegmental area and brain regions known to participate in the control of maternal behaviour and the global deficits in maternal behaviour following ventral tegmental area lesions, it is likely that this region will receive further experimental attention.

Despite the number of studies in the area, our understanding of the neural mechanisms and pathways underlying maternal behaviour is far from complete. As pointed out by Lamb (1975) and Slotnick (1975), studies of neural control of maternal behaviour have been fragmentary and no attempts have been made to integrate the available findings. The lesion technique is of limited value because lesions, in addition to destroying nuclei, also destroy fibers of passage. The knife cut technique (see below) as employed in studies of feeding and sex behaviours (e.g. Malsbury, Strull, and Daood, 1978; Sclafani and Berner, 1977) in combination with more refined and systematic behavioural testing should prove to be invaluable in advancing our understanding of the neural mechanisms and pathways mediating maternal behaviour.

Recent investigative efforts have centered around hypothalamic control of maternal care. Numan (1974) was the first to report medial preoptic area (MPOA) involvement in the control of maternal behaviour in the rat. Rats sustaining lesions of this area failed to build nests or retrieve pups and spent less time nursing than controls. A similar deficit was observed after parasagittal knife cuts along the MPOA and medial anterior hypothalamus (MAH) (Numan, 1974). These findings were subsequently replicated in a number of other rat studies (Jacobson, Terkel, Gorski, and Sawyer, 1980; Smotherman, Hennessey, and Levine, 1977; Terkel, Bridges, and Sawyer, 1979).

In rats, increasing levels of estrogen in combination with decreasing progesterone levels are thought to mediate the rapid onset of maternal behaviour at parturition (Moltz et al., 1970). Because the MPOA and MAH (collectively referred to as the MPOA-MAH continuum) contain estrogen concentrating cells (Pfaff and Keiner, 1973; Stumpf, Sar, and Keefer, 1975, in the rat; Krieger, Morrell, and Pfaff, 1976, in the hamster) it seemed plausible that the MPOA-MAH is the target tissue mediating estrogenic modulation of maternal behaviours. This hypothesis was confirmed in an experiment where estrogen implants in the MPOA-MAH reduced the latency to maternal behaviour in nulliparous rats (Numan, Rosenblatt, and Komisaruk, 1977).

Lesions of the MPOA-MAH and transection of its lateral connections result in a failure to build nests and retrieve pups. However, sniffing and licking of the pups, and to some extent, nursing behaviour remain intact (Jacobson et al., 1980; Terkel et al., 1979). On this basis these workers concluded that these manipulations only disrupt active components of maternal behaviour; namely, those maternal behaviours that the dam must initiate by exploring the environment. Such behaviours are similar to proceptive aspects of female mating behaviour and male mating behaviour in that they also must be initiated by the animal. Male copulatory behaviour, like maternal behaviour, is dependent on the integrity of the MPOA-MAH (Giantonio, Lund, and Gerall, 1970; Heimer and Larson, 1968). Implants of gonadal steroids in this area readily reactivate male copulatory behaviour in castrated rats (Davis and Barfield, 1979) and hamsters (Lisk and Bezier, 1980). Ultrasonic vocalization is a proceptive component of the female hamster's mating sequence currently receiving experimental attention. In hamsters ultrasonic vocalization is an estrogen dependent behaviour that likely serves to communicate sexual receptivity and location to nearby males (Floody, Pfaff, and Lewis, 1977; Floody and Pfaff, 1977b; Floody, 1979). A preliminary report indicates that the MPOA also mediates male-soliciting ultrasonic calling in the hamster (Merkle and Floody, 1979). These findings cast some doubt as to the specificity of the deficit resulting from MPOA-MAH damage. The effects of the destruction of this tissue may be related to some general inability to initiate various reproductive behaviours, rather than a deficit specifically related to maternal behaviour.

In contrast to feeding and sex behaviours, little is known about the hypothalamic circuitry underlying rodent maternal behaviour. The MPOA and MAH appear to have reciprocal connections (Conrad and Pfaff, 1976a; 1976b). Additionally, this contium receives afferents from and sends efferents to nucleus accumbens (Conrad and Pfaff, 1976a; 1976b), the septum (Millhouse, 1969), and the ventral tegmental area (Phillipson, 1979; Simon, Le Moal, and Calas, 1979) through the medial forebrain bundle; and also has reciprocal connections with the amygdala via the stria terminalis (De Olmos and Ingram, 1972; Conrad and Pfaff, 1976a; 1976b). The above mentioned structures all have been implicated with the control of maternal behaviour in the rat (Fleischer and Slotnick, 1978; Fleming et al., 1980; Gaffori and Le Moal, 1979; Smith and Holland, 1975). These neuroanatomical studies show that the MPOA-MAH projects to and receives input from many extrahypothalamic regions. Work to describe and identify pathways important for maternal behaviour has already begun.

Numan (1974) initially concluded that the dorsal connections of the MPOA-MAH were not critical because horizontal transection of the medial corticohypothalamic tract did not disrupt maternal behaviour in rats. Subsequently, it was discovered that horizontal transection of the fornix disrupts rat maternal behaviour, indicating that dorsal pathways may be important (Steele, Rowland, and Moltz, 1979). Moreover, Numan himself later discovered that horizontal knife cuts severing the dorsal connections of MPOA-MAH can produce impairments in nursing behaviours

(Numan and Callahan, 1980). The effects of frontal-plane cuts severing the anterior or posterior connections of the MPOA have also been evaluated by Numan and Callahan (1980). Only the anterior coronal cuts were reported to disrupt maternal behaviour. The maternal deficits produced by these cuts were accompanied by weight loss and hypoactivity. The maternal deficit in these animals, therefore, was likely a secondary effect of the cuts. That the lateral connections of the MPOA-MAH are essential for the expression of maternal behaviour has been firmly established in the rat (Numan, 1974; Smotherman et al., 1977; Terkel et al., 1979) and extended to the hamster (Marques, Malsbury, and Daood, 1979). Lesions of the lateral hypothalamus which encroach on the parafornical medial forebrain bundle (MFB) have been reported to also disrupt maternal behaviour (Avar, Monos, Kurey, Nagy, and Bukulya, 1973). This suggested to Numan (1974) that the MPOA exerts its influence over maternal behaviour through its lateral connections with the MFB. Numan cites experimental data demonstrating that dorsolateral hypothalamic stimulation elicits components of nest building (Roberts and Carey, 1965) and pup retrieval (Zarrow, Gandleman, and Denenberg, 1971) to support this argument. Furthermore, Numan (1974), in a preliminary study of degenerated fibers following sagittal cuts along the MPOA-MAH, found such fibers in the MFB.

The MPOA and MAH have long axonal projections crossing the MFB and lateral hypothalamus (Conrad and Pfaff, 1976a; 1976b) which would have also been severed by the sagittal cuts in the above mentioned studies (Marques et al., 1979; Numan, 1974; Terkel et al., 1979). This finding casts some uncertainty on Numan's hypothesis that the lateral projections of the MPOA critical for maternal behaviour ascend or descend through the

MFB. In a recent study of sexual receptivity in the female hamster (Malsbury, Marques and Daood, 1979) the mediolateral position of sagittal plane knife cuts along the ventromedial nucleus of the hypothalamus (VMN) was varied such that some cuts were placed at the medial border of the MFB and other cuts were placed at the lateral border of the MFB, sparing VMN-MFB connections. Both cuts were in a position to disrupt VMN afferents/ efferents travelling in the region of the supraoptic commissures (SOC). Each cut was effective in reducing or eliminating receptivity. In this way, these workers were able to demonstrate the importance of SOC connections for lordosis.

The following study was undertaken to determine whether SOC connections, rostral to those essential for sexual receptivity, are also critical for maternal behaviour. It has already been established that sagittal knife cuts placed medial to the MFB along the MPOA-MAH disrupt normal maternal activity in both the virgin and lactating hamster (Marques et al., 1979). It was of interest to determine whether cuts placed at the same rostrocaudal position as in the above study, but lateral to the MFB, would have the same behavioural consequences as medially placed cuts. In addition to the more traditional maternal behaviours (ie., pup retrieval and nest building), it was also of interest to see whether these cuts would disrupt other types of maternal behaviour; specifically, food hoarding and the ability to regulate litter size in accordance with whether or not animals are given the opportunity to hoard (Miceli and Malsbury, unpublished manuscript). Lastly, since lesions of the MPOA depress ultrasound production (Merkle and Floody, 1979), animals were also tested for this behaviour in order to determine whether lateral connections are also important for ultrasonic calling.

METHOD

Subjects

Experimental and pup donor hamsters were purchased from the Canadian Breeding Laboratories which obtain their stocks from the Lakeview, New Jersey hamster colony. At the onset of the experiment animals were 90-110 days old and weighed 90-130 g.

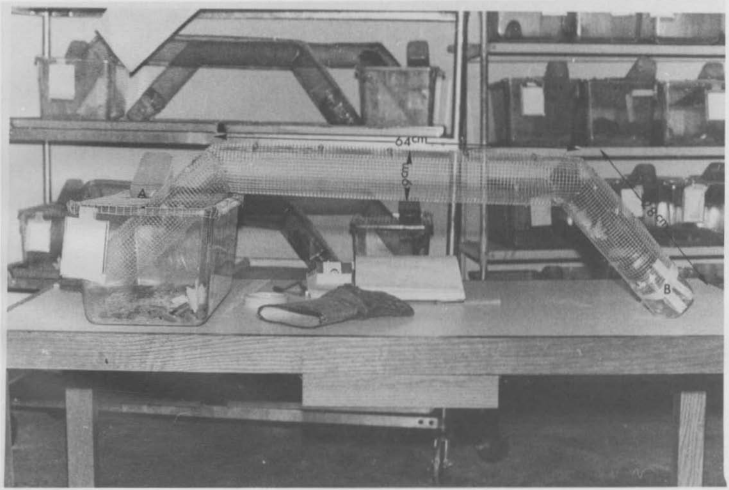
Housing and Maintenance

Prior to the preoperative vocalization test (see below) animals were transferred from suspended wire-mesh cages and permanently housed in plexiglas tub cages (24 x 44 x 20 cm). These cages were modified with a lid allowing a wire-mesh tunnel to adjoin the cage with a food jar (see Figure 1). Animals were provided with woodchips and paper towelling for nesting material. The colony room was maintained on a 14:10 hr illumination cycle with lights on at 1600 hr. Room temperature was maintained at an average of 23°C. Water was available ad lib and Purina Rat Chow was available as described below.

Experimental Design

Sixteen animals received bilateral sagittal knife cuts immediately lateral to the MPOA-MAH. These cuts were intended to be placed medial to the MFB. Animals with such cuts are referred to as the Near Lateral (NL) hamsters. Another 16 animals sustained cuts identical to the NL animals in the rostrocaudal extent, but lateral to the MFB, and are referred to as Far Lateral (FL) hamsters. Eight animals served as surgical controls. Across the surgical conditions, half the animals were allowed to construct and maintain a food hoard; the others received

Figure 1 Housing and hoarding apparatus for experimental hamsters.
A. Location of food trough for Sham-Hoard animals.
B. Location of food jar for Hoard group animals and the "sham hoard" for Sham-Hoard hamsters.


64 cm
9 cm
28 cm
A
B

daily food rations, thus yielding a surgical condition x hoarding condition factorial design.

Surgery

Surgery was performed under sodium pentobarbital (65 mg/kg) anesthesia. Within 10 days after all preoperative testing, animals were placed in a stereotaxic instrument with the head adjusted such that the midline suture between bregma and lambda was on a horizontal plane. The knife cuts were placed according to a skull-flat atlas of the hamster hypothalamus (Malsbury, 1977). Coordinates for NL cuts were 1.7 mm anterior to the bregma and 1.1 mm lateral to the midline; and for FL cuts, 1.7 mm anterior to bregma and 2.1 mm lateral to the midline.

The knife assembly and carrier used to make the cuts are described by Scouten, Cegavske and Rozboril (1981). For both cuts (NL and FL) a 30 ga cannula was lowered 4.7 mm from the dura, at which point a 0.1 mm tungsten wire was extruded 1.8 mm, facing caudally in the sagittal plane. The cannula was then lowered 2.2-2.4 mm further and returned to 4.7 mm below the dura. At this point, the wire was retracted back into the cannula and the cannula withdrawn from the brain. Control animals had the cannula lowered 4.7 mm below the dura, but the wire was not extended nor was the cannula lowered further. Half of the surgical shams had the cannula lowered at 1.1 mm lateral to the midline, and the other half at 2.1 lateral to the midline. After knife cuts or sham cuts were made bilaterally, holes were sealed with bone wax and wounds closed with silk sutures.

Feeding and Hoarding Arrangements

The hoarding manipulation became effective once animals were housed in the hoarding apparatus. Those animals allowed to hoard were given free access to a food jar holding approximately 100 pellets (400-500 g). These animals were free to feed and hoard from this jar. Hoarded food remained undisturbed until the weekly cage changes or just before the maternal tests described below. At these times, a fresh cage with a replenished food jar was provided, allowing the hoarding process to begin again. These groups are referred to as the Hoard (HD) groups (Sham-HD, NL-HD, and FL-HD). Other groups were given what has been called a "Sham-Hoard" (Miceli and Malsbury, unpublished manuscript), that is, a jar of pellets identical to that in HD groups except that it was sealed with a perforated lid so that these animals could see and smell the food, but not feed or hoard from the jar. Food for these animals was provided over the cage in a trough with the water bottle. Throughout the experiment these animals were given a daily ration of 7-9 pellets (30-40 g). Pellet remains from the previous day were removed when fresh feed was provided. These animals formed the Sham-Hoard (SH) groups (Sham-SH, NL-SH, and FL-SH).

Vocalization Tests

Preoperatively, virgin animals were tested for ultrasonic vocalizations prior to the preoperative maternal tests. These tests were conducted in a dimly lit room away from other animals. Hamsters were tested in their home cages with the hoarding apparatus removed.

A microphone was held perpendicularly approximately 10 cm above the top of the cage. Ultrasonic calls were made audible through stereophonic headphones connected to a Holgate ultrasonic receiver, tuner adjusted at 35 kHz. The hamsters were given at least five min to habituate to the new environment before a male was introduced to their cages. The male was removed from the female's cage after it had made two mounts or after five min, which ever occurred first. Immediately after males were removed from females' cages vocalizations were monitored for five min.

Postoperative vocalization tests were identical to the preoperative tests except that they occurred after the postoperative virgin-maternal tests and males were allowed to impregnate the females after the vocalization observations had been made. Both tests were conducted on the day of estrus.

Virgin Maternal Tests

All animals were given series of pre- and postoperative virgin maternal tests. In preoperative tests, three 0-4 day old foster pups were introduced to each animal. The pups were placed on the cage floor in a corner diagonally opposite to the subject's established nest site, while the subject was positioned in the tunnel. In later tests, in which some animals did not build nests, pups were placed in a corner diagonally opposite to where the female was situated before the test. The test was begun once the subject stepped down from the tunnel and the subject's four paws touched the cage floor. At this point the subject's behaviour was noted for eight min. A cross-section of the subject's behaviour was provided by noting what the animal was doing at five sec intervals. Relevant items in the behavioural inventory included the following pup-directed activities:

APPROACHING and WITHDRAWING from pups

SNIFFING, LICKING, or MOUTHING pups

RETRIEVAL of pups

NEST BUILDING and REPAIRING

LACTATING POSTURE or CROUCHING over pups

BITING-ATTACKING and EATING pups.

Pups not attacked or eaten during this test period were left 24 hr with the subjects, at which point subjects were retested in the same manner with three new foster pups. Those animals which cannibalized on the first test were also retested 24 hr later with three freshly fed foster pups. Again, those animals which had not cannibalized on the second test were left with the foster pups for another 24 hr. Prior to the second test and 24 hr later, spot-checks were made in order to observe the relative positions of the animal, nest, and if applicable, pups. The day before the first test, cages were changed and hamsters were given fresh strips of paper towelling with which to build nests. The day after the second test the quality of the nest built over that period was rated on a three point scale. Two points were given to nests with finely shredded, tightly packed paper towelling. Zero points were recorded in those cases where paper towelling was not gathered or shredded. Nests of intermediate quality were given one point. Hoarding data were collected for animals in the HD groups on the same occasions as the nesting observations. The number of pellets in a hoard, if one was present, and its location within the cage were noted. A hoard is operationally defined as 10 or more pellets removed from the food jar and piled or tightky packed in some other portion of the animal's living quarters. Only pellets weighing more than two g qualified as hoarded pellets. Because of varying numbers of pellets initially held in jars (attributable to general differences in pellet size), 100 pellets were counted in those cases where all the pellets were transported from the jar. These procedures were repeated postoperatively.

Gestation and Pospartum Observations

On Day 15 gestation nesting and hoarding observations were made as described above. In this hamster colony animals gave birth between 1800 hr of one evening and 0600 hr the next morning. During this period all but two animals were monitored at 10 min intervals. This was done in order to determine initial litter size and to detect early postpartum cannibalism. The end of parturition was determined by gently squeezing the animals' midsection until no further pups could be detected in utero. For two animals this monitoring was not possible. The morning of, or after, parturition is designated as Day 0 lactation. On Days 1 and 2 lactation behavioural observations were made as in the virgin tests. Those animals with surviving pups were tested with three pups from their own litter, while those which had cannibalized their entire litter prior to the tests were tested with three foster pups. Where appropriate, animals had the remainder of their litters returned to them at the end of tests. Nesting and hoarding observations were repeated on Days 3, 9, and 15 lactation.

Body Weights

Subjects were weighed pre- and postoperatively (at the time of each vocalization test), on Day 16 gestation and on each successive day of lactation to Day 15. Surviving litters were also weighed on each day of lactation.

Histology

After all observations were made, animals were deeply anesthetized with sodium pentobarbital and perfused intracardially with saline followed by 10% phosphate buffered formalin. Brains were removed from the skull and stored in formalin for at least 12 days. Frozen brains were sectioned at 50 microns in the frontal plane and stained with hot formol-thionin (Donovick, 1974).

RESULTS

Histology

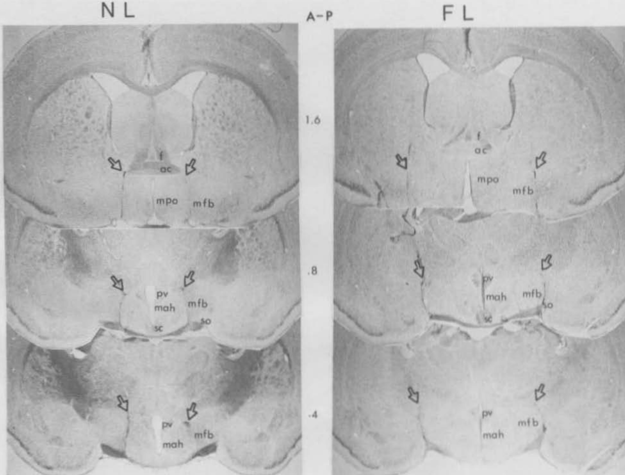
Histological examination of the brain tissue was conducted with the evaluator blind to individual subject's behaviour. In order for cuts to be considered complete they had to reach the base of the brain and begin rostral to the anterior portion of the paraventricular nucleus. It was decided *a priori* that those animals with cuts that did not meet these criteria would be placed in appropriate (HD or SH) surgical control groups. This was the case for one animal initially in the FL-HD group whose cuts began too caudal and did not reach the base of the brain. Because dorsolateral connections of the MPOA-MAH are considered important for maternal behaviour in rats (Terkel et al., 1979), cuts were considered to have begun anteriorly at the rostrocaudal level at which they reached a 1 mm length D-V.

Dorsally, typical cuts began just under, or in a few cases, infringing on the ventral portion of the anterior commisure at the rostral extent, and slightly above the dorsal paraventricular nucleus at the caudal extent. This was the case for both NL and FL cuts. With the above exception, all cuts reached the base of the brain doing no damage to the optic tract anteriorly, and minimal damage posteriorly. Cuts in both groups were reasonably symmetrical rostrocaudally. However, there was some asymmetry mediolaterally. In all but four cases (one in the NL-SH; two in the FL-HD; and one in the FL-SH groups) the asymmetry was not to the extent where the cut was medial to the MFB on one side and lateral to the MFB on the contralateral side. The four animals with the mediolaterally asymmetrical cuts were dropped from their original groups and pooled to form group ASYM (asymmetrical) for some statistical analyses. Typical NL cuts were 0.2-0.3 mm medial to the supraoptic nucleus anteriorly, and immediately lateral to the fornix posteriorly. FL cuts were lateral to or at the lateral edge of the supraoptic nucleus. Rostrocaudally, both types of cut began at the caudal level of the anterior commisure and ended caudally at the level of the paraventricular nucleus-rostral tip of the ventromedial hypothalamic nucleus. Illustrative histology is shown in Figure 2.

Vocalizations

Seven of the NL (four in the HD group and three in the SH group) animals either did not show behavioural estrus or normal cyclicity within 10 days after surgery. To overcome this problem, these animals were hormone primed prior to the postoperative vocalization test and mating. Estradiol benzoate (62 µg/kg) was administered 47 hr before testing and progesterone (3 mg/kg) was administered 5-7 hr prior to testing. Hormones were given by subcutaneous injection in approximately 0.1 ml of oil. These animals showed receptivity during the postoperative

Figure 2 Photomicrographs of frontal sections showing the locations of bilateral sagittal-plane cuts from a female of the NL group (left column) and FL group (right column). The dorsal portions of the cuts are indicated by black arrows. The rostrocaudal (AP) coordinates are taken from Malsbury (1977). ac, anterior commissure; f, fornix; mah, medial anterior hypothalamus; mfb, medial forebrain bundle; mpo, medial preoptic area; pv, paraventricular nucleus; sc, suprachiasmatic nucleus; so, supraoptic nucleus.


NL
A-P
FL
1.6
.8
.4
f
ac
mpo
mfb
pv
mah
sc
so

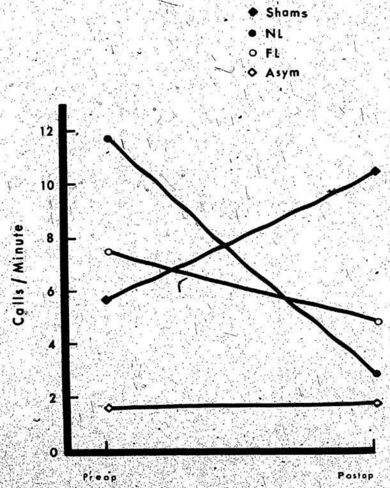
test, and all but one subsequently became pregnant. For these reasons they were not dropped from the study.

The hoarding condition did not influence vocalizations. Thus, HD and SH groups were combined for statistical analysis. The animals with asymmetrical cuts were pooled fro comparison to the SHAM, NL, And FL groups. A two-way analysis of variance with repeated measures (PREOP vs. POSTOP trials) conducted on vocalization rates (calls per minute) failed to yield overall group and trial effects. A group x trials interaction, however, was highly significant, $\underline{F}\ (2, 30) = 6.33$, $\underline{p} < .005$. Post-hoc pairwise comparisons (Tukey A tests) of postoperative group means revealed no significant difference among the NL, FL, and ASYM groups. SHAMS, however, emitted more ultrasonic calls postoperatively than NL, FL, or ASYM hamsters, $\underline{p} < .01$ (see Figure 3).

Correlation of Histology with Vocalizations

Approximately 40% of the cuts (30% of FL cuts and 50% of NL cuts) began at the level of the MPOA, and the remaining 60% begain further caudal at the rostral level of the MAH (as defined in the Malsbury [1977] atlas). There were no significant differences between those animals with cuts extending rostrally to the MPOA and those animals whose cuts began at the level of the MAH. The two-factor analysis of variance also indicated that the rostrocaudal x mediolateral placement factors did not interact. Further examination of the data revealed that those animals with cuts extending from the level of the rostral tip of the suprachiasmitc nucleus to the level just anterior to the rostral portion of the ventromedial nucleus showed the lowest postoperative call rates.

Figure 3 Mean rates of ultrasonic calling before (Preop) and after surgery (Postop). Preoperative group differences may be attributed to the re-grouping of some subjects after histology. These preoperative differences, however, are not significant, $\underline{p} > .05$ (Tukey A tests), because of a large within-groups variance.


Shams
NL
FL
Asym
Calls / Minute
0
2
4
6
8
10
12
Preop
Postop

Prepartum Maternal Behaviour

Preoperatively, virgin animals either cannibalized or retrieved foster pups on their initial contact with them. Appproximately half the animals which cannibalized on the first preoperative virgin test showed a different response on the second test (i.e, either pup retrieval or no response towards pups). Retrievers on the first test were consistent with their pup directed response on the second test. Because virgin hamsters that initially cannibalize and later retrieve pups show consistent retrieval after the transition (Miceli and Malsbury, in preparation), the criteria for maternal behaviour chosen for this study was that an animal had to have shown pup retrieval by the second test, or if no response was shown during the second test, animals had to have shown some evidence of maternal behaviour between the second test and the spot-check 24 hr later. Three animals (one in the FL-SH group and two in the NL-HD group) met the second criterion for maternal behaviour. On the spot-check 24 hr after the second test, pups were found in nest, warm under each of the experimental adults. Retrievel as a criterion for maternal behaviour is appropriate because, as demonstrated in Table II, those animals which retrieved during the tests showed other components of maternal behaviour.

Preoperatively, there were no significant differences in the type of response shown towards foster pups among the surgical groups. Those animals with the hoarding opportunity, however, were more likely to behave maternally than animals given daily food rations, χ^2 (1) = 4.33, $p < .05$. These results are summarized in Table I.

The same criteria for maternal behaviour were adopted for the

Table I

Preoperative Pup-Directed Responses

Group	n	% Maternal [1]	% Cannibalizing [2]
Sham			
Hoard	5	80	20
Sham-Hoard	4	25	75
Near Lateral			
Hoard	8	100	00
Sham-Hoard	7	29	71
Far Lateral			
Hoard	5	60	40
Sham-Hoard	7	29	71

[1] See text for criterion for maternal behaviour

[2] Cannibalizing on both tests

Table II

Mean Frequency and Latency of Behavioural Items on the Second Preoperative Maternal Test

		Behavioural Item				
Group	n	Sniff (f)	Lick (f)	Mouth (f)	Retrieval (f)	Retrieval Latency (secs)
Maternal	26	12.6	9.5	2.8	16.7	128.4
Cannibal	14	1.8	—	—	—	—

		Behavioural Item				
Group	n	Crouch (f)	Nest Repair (f)	Bite (f)	Pup Eat (f)	Attack Latency (secs)
Maternal	26	2.6	2.7	—	—	—
Cannibal	14	—	1.4	10.6	17.4	25.9

(f), frequency
(secs), seconds

postoperative virgin maternal tests. Postoperatively, the effects of the hoarding opportunity did not change from the preoperative period. HD groups had more maternal animals than SH groups, χ^2 (2) = 7.91, $p < .05$. While surgical sham groups gained maternal animals postoperatively, both NL and FL groups had animals that were previously maternal become cannibals after surgery. Analyses of the postoperative data revealed that NL and FL groups had higher proportions of cannibals than Shams, χ^2 (4) = 18.95, $p < .001$, and that NL and FL groups did not differ in proportions of cannibals and maternal animals.

It can be seen in Table III that the disruptive effects of the knife cuts are more robust in the Sham-Hoard groups. For instance, 25% of the NL-HD and 40% of the FL-HD animals responded maternally during the postoperative tests, while no animals in the NL-SH and FL-SH groups did so. Small sample sizes did not allow statistical comparisons of either maternal or cannibalistic behaviours displayed by intact and knife-cut animals. By casual observation, the maternal behaviours of knife-cut animals did not appear to differ from those of sham-operated animals. Similarly, the cannibalistic behaviours of knife-cut animals did not appear to differ from those observed during preoperative testing.

Prepartum Nest Building

Nesting activity did not vary with the hoard condition throughout the course of the experiment. For this reason, the hoarding groups were collapsed for nesting comparisons. Preoperatively, the majority of animals built some sort of a nest (of either the type 1 or type 2 quality). Postoperatively, NL animals showed the greatest disruption of nest building. The majority of NL animals did not gather or shred

Table III
Postoperative Pup-Directed Responses

Group	n	% Maternal	% Cannibals	% No Response
Sham				
Hoard	5	100	00	00
Sham-Hoard	4	75	25	00
Near Lateral				
Hoard	8	25	50	25
Sham-Hoard	7	00	100	00
Far Lateral				
Hoard	5	40	60	00
Sham-Hoard	7	00	100	00

Table IV

Mean Frequency and Latency of Behavioural Items on the Second Postoperative Maternal Test

		Behavioural Item				
Group	n	Sniff (f)	Lick (f)	Mouth (f)	Retrieval (f)	Retrieval Latency (secs)
Maternal*	8	7.6	4.9	0.8	73.1	150.6
Cannibal**	21	4.3	0.4	—	—	—

		Behavioural Item				
Group	n	Crouch (f)	Nest Repair (f)	Bite (f)	Pup Eat (f)	Attack Latency (secs)
Maternal	8	0.0	9.5	—	—	—
Cannibal	21	—	1.4	12.4	16.0	76.1

* Maternal animals in sham operated groups

** Combined cannibals in NL and FL groups

(f), frequency

(secs), seconds

strips of paper towelling (80% had a nest score of 0). In comparison, only 25% of the animals in the FL groups and no SHAMS had a nest score of 0. These differences are significant, $\underline{\chi}^2$ (4) = 24.16, $\underline{p}$ < .001. As shown in Figure 4 (top), FL animals showed only a mild impairment of nest building. Most of these animals had a nest score of 1 (significantly more than NLs or SHAMs), though none built good (type 2) nests. Nesting observations made on Day 15 gestation were also statistiically analyzed. All groups improved somewhat on nest quality, however, the nesting deficit persisted in NL animals but not in FL hamsters.

Body Weight

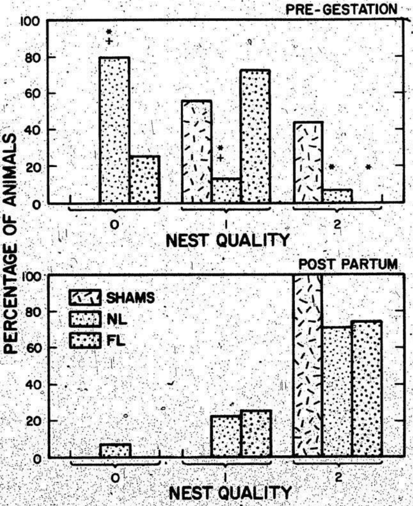
A three-way analysis of variance with repeated measures was used to test for differences in mean body weight among the groups at the pre-operative, postoperative, and Day 0 lactation weighings. All groups gained weight over time, $\underline{F}$ (2, 58) = 11.57, $\underline{p}$ < .001. Overall, body weight did not differ with the hoarding condition, however, SHAM and FL animals with the hoarding opportunity did gain more weight from the pre- to postoperative period than their counterparts given daily food rations, $\underline{F}$ (2, 58) = 7.36, $\underline{p}$ < .002. NL-HD and NL-SH animals showed comparable weight gains from the pre- to postoperative periods. Weight gains over gestation (i.e., the difference between postoperative and Day 0 lactation body weights) were comparable across all groups (see Figure 5).

Lactational body weights of surgical shams were also statistically examined. A two-factor analysis of variance with repeated measures comparing body weights of Sham-HD and Sham-SH animals at Days 0, 5, 9, and 15 lactation and Tukey A test comparing the groups at these time points reveal the following: Both groups lost weight over lactation,

Figure 4 Percentage of animals in each group having built nests of different qualities during two postoperative periods.

* different from shams, $\underline{p} < .01$.

+ different from FLs, $\underline{p} < .01$.


PRE-GESTATION
POST PARTUM
PERCENTAGE OF ANIMALS
NEST QUALITY
NEST QUALITY
SHAMS
NL
FL
100
80
60
40
20
0
0
1
2

and Sham-HD animals were consistently heavier than Sham-SH animals, $F\ (1, 17) = 33.8$, $p < .001$, and $F\ (5, 35) = 17.21$, $p < .001$, respectively. A group x days interaction was not found. The major finding from the post-hoc comparisons was that neither group had dropped to below premating body weight levels by Day 15 lactation.

Food Hoarding

A two-way analysis of variance with repeated measures was used to test for differences in the number of pellets hoarded by Sham-HD, NL-HD and FL-HD groups at PREOP, POSTOP, Day 15 gestation, and Days 3 and 15 lactation. No significant differences among the groups were found but hoarding did increase over trials, $F\ (4, 56) = 44.42$, $p < .001$. Subsequent post-hoc comparisons (Tukey A tests) indicated that in each group the number of pellets hoarded did not change from the pre- to postoperative periods. All groups hoarded more during gestation and lactation than during both the pre- and postoperative premating periods $p < .001$. No significant differences between gestation and the end of lactation were found. These data are summarized in Table V.

Postpartum Nest Building

All groups showed improvement in nest quality during the postpartum period (see Figure 4, bottom). At Day 3 postpartum, there were no differences in the quality of nests built by animals of different surgical groups. It should be noted, however, that while NL animals gathered and shredded strips of paper towelling, the nests built by these animals were deficient in a manner that the a priori chosen rating criterion could not detect. Whereas, SHAM and FL animals had built their nests over,

Figure 5 Body weights of animals at various phases of the experiment.

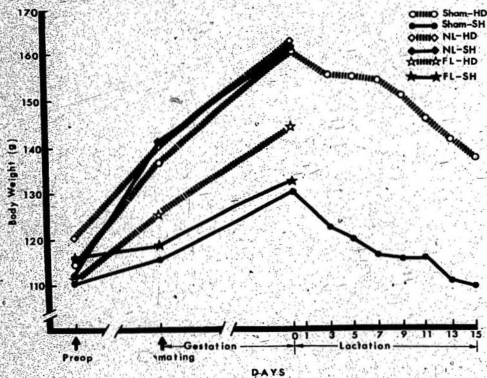

Sham-HD
Sham-SH
NL-HD
NL-SH
FL-HD
FL-SH
Body Weight (g)
170
160
150
140
130
120
110
Preop
mating
Gestation
Lactation
0 1 3 5 7 9 11 13 15
DAYS

Table V

Mean Pellets Hoarded at Various Periods of the Reproductive Cycle

		Number of Pellets Hoarded				
Hoard Group	n	Preop	Postop	Gestation	Postpartum Day 3	Postpartum Day 15
Sham	5	9.7	13.7	84.0	79.4	100.0
Near Lateral	7	6.5	10.8	62.4	60.5	60.2
Far Lateral	5	20.7	7.2	89.3	80.5	100.0

and reinforced nest walls with woodchips, all but two of the NL animals had cleared the nesting area of woodchips and built their nests over the bare cage floor.

Postpartum Maternal Behaviour

On postpartum maternal tests, groups did not differ in the type of response shown towards pups. Most animals retrieved pups during the tests (see Table VI). Two-factor analyses of variance on the behavioural items and latencies indicated that groups differed only in one measure (see Table VII). SH group animals showed longer retrieval latencies than HD group animals. This, however, is attributable to the fact that those animals not retrieving during a test were assigned a latency of eight minutes (the duration of test). There were, of course, more of these cases in the SH groups than in HD groups. Pups were weighed and examined for general health daily. Surviving pups of animals from all groups had milk bands across their abdomen and appeared to be growing normally.

A three-way analysis of variance with repeated measures was conducted to determine significance of differences in litter size among the groups at parturition, and Days 5, 9, and 15 lactation. In two cases (one in the NL-HD and the other in the NL-SH group) determination of pups present at parturition was not possible. These missing values were determined by a least-squares estimate and were included in the statistical analyses. Bias introduced to treatment sums of squares by these estimates was partialled out by a statistical procedure described in Snedecor (1956). A third animal (from the NL-HD group) did not become pregnant and was not included in any of the postpartum analyses. Litter

Table VI

Pup-Directed Responses on the Second Postpartum Maternal Test[1]

Group	n	% Maternal[2]	% Cannibals[3]	% Both Behaviours[4]
Sham				
Hoard	5	100	00	00
Sham-Hoard	4	75	25	00
Near Lateral				
Hoard	7	86	00	14
Sham-Hoard	7	57	14	28
Far Lateral				
Hoard	5	80	00	20
Sham-Hoard	7	57	43	00

[1] These results are identical to those of the first postpartum test.

[2] Animals retrieving all three test pups to the nest site during the test.

[3] Animals cannibalizing all three test pups during the test.

[4] Animals retrieving one or more pups but cannibalizing the remaining pups or retrieving all pups but cannibalizing one or more thereafter.

Table VII

Mean Frequency and Latency of Behavioural Items on the Second Postpartum Maternal Test

Group	n	Behavioural Item: Sniff (f)	Lick (f)	Mouth (f)	Retrieve (f)
Sham					
Hoard	5	2.0	6.0	5.0	35.0
Sham-Hoard	4	0.8	2.8	1.5	43.2
Near Lateral					
Hoard	7	6.3	2.5	4.5	17.9
Sham-Hoard	7	2.5	1.5	3.4	18.8
Far Lateral					
Hoard	5	1.7	1.7	2.8	13.4
Sham-Hoard	7	0.6	0.6	1.7	14.7

Group	Behavioural Item: Retrieval Latency (secs)	Crouch (f)	Nest Repair (f)	% of Animals With a Litter Surviving to Day 15 Lactation
Sham				
Hoard	11.0	7.6	16.2	100
Sham-Hoard	147.2*	3.0	11.8	75
Near Lateral				
Hoard	18.6	2.9	13.4	71
Sham-Hoard	90.0*	0.7	8.5	00
Far Lateral				
Hoard	21.0	3.5	12.7	80
Sham-Hoard	186.2*	1.3	7.9	29

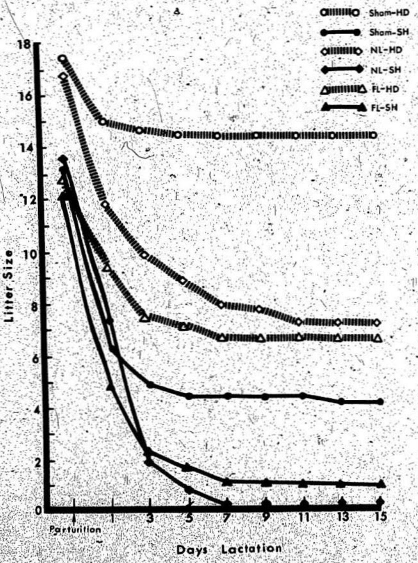
(f), frequency
(secs), seconds
*Greater than corresponding Hoard group, $p \leq .01$

size for all groups decreased over lactation, $\underline{F}$ (8, 232) = 84.96, $\underline{p} < .001$. Overall, sham operated animals had larger litters than knife cut animals, $\underline{F}$ (2, 29) = 5.46, $\underline{p} < .01$, and those animals given the opportunity to hoard had larger litters than those given daily food rations, $\underline{F}$ (2, 29) = 33.49, $\underline{p} < .001$. Surgical factor x hoarding factor and surgical factor x hoarding factor x time factor interactions were not significant. Time factor x surgical factor and time factor x hoarding factor interactions, on the other hand, were significant, $\underline{F}$ (16, 232) = 3.72, $\underline{p} < .001$ and $\underline{F}$ (8, 232) = 6.72, $\underline{p} < .001$, respectively.

To make the above interactions more meaningful, the groups were compared for mean litter size at parturition and Day 15 lactation (i.e., tests were made on simple main effects, Winer, 1971). Litter size at parturition did not differ among the surgical groups; however, those animals with the hoarding opportunity did have larger litters than animals on daily food rations, $\underline{p} < .02$. At Day 15 lactation each surgical group with the hoard had larger litters than their respective sham-hoard counterparts, $\underline{p} < .001$, in each case. NL and FL groups with hoards had smaller litters than the Sham-HD animals, but larger litters than hamsters in the Sham-SH group, $\underline{p} < .001$, in each instance. NL and FL groups did not differ from each other at Day 15. NL and FL hamsters with sham-hoards had smaller litters than any of the other groups, $\underline{p} < .001$, for each comparison. The difference between these two groups at Day 15 lactation was not significant.

It should be mentioned that the decreasing litter sizes were largely due to cannibalism. Frequently, dead pups were found during the daily weighings. In these cases there was evidence of some degree of cannibal-

Figure 6. Mean litter size throughout the first 15 days of lactation.



Sham-HD
Sham-SH
NL-HD
NL-SH
FL-HD
FL-SH
Litter Size
18
16
14
12
10
8
6
4
2
0
Parturition
1
3
5
7
9
11
13
15
Days Lactation

ism as these pups were partially consumed. More often, pups present on the previous day would be found missing during the daily inspections.

Correlation of Histology with Maternal Behaviour

As with ultrasonic vocalizations, animals were divided into subgroups; those whose cuts extended rostrally to the MPOA and those whose cuts began posterior to the MPOA. A two-factor (rostrocaudal x mediolateral placements of knife cuts) analysis of variance was conducted on Day 15 lactation litter size. Again, no differences between NL and FL litter sizes were found. Furthermore, those animals whose cuts began at the level of the MPOA reared the same sized litters as those with the slightly more posterior cuts. The analysis did not yield a significant mediolateral x rostrocaudal cut placement interaction. These results are not confounded by the hoarding condition because the distribution of hoarders and sham-hoarders in the MPOA and MAH subgroups was reasonably even.

DISCUSSION

Parasagittal knife cuts along the MPOA-MAH reduced rates of ultrasonic calling. Postoperative call rates of NL and FL animals were not significantly different from each other or from those of ASYM hamsters. The data suggest that NL and FL cuts disrupted a common pathway important for ultrasonic calling. Recently, Merkle and Floody (1979) found that lesions of the MPOA depressed ultrasound production in female hamsters. In the present study, however, the most effective rostrocaudal position of knife cuts was at the level of the suprachiasmatic nucleus, caudal to the MPOA. Since Merkle and Floody's data are reported in abstract form, it is not known whether their MPOA lesions encroached caudally on the anterior hypothalamus.

These data demonstrate that hypothalamic lesions and knife cuts can dissociate proceptive and receptive components of the female hamster's mating behaviour. In Merkle and Floody's (1979) study lesions of the MPOA reduced ultrasonic calling but did not disrupt lordosis, and conversely, lesions of the ventromedial nucleus disrupted lordosis while leaving ultrasonic calling unaffected. In the present study, knife cuts at varied mediolateral positions along the MPOA-MAH reduced ultrasonic calling. Other studies have shown that similar knife cuts (NL and FL) along the ventromedial nucleus can eliminate or reduce lordosis in the hamster (Malsbury et al., 1979; Marques et al., 1979).

The MPOA and MAH both have axon groups which descend in the MFB and project to the midbrain central grey (Conrad and Pfaff, 1976a; 1976b). The central grey reciprocates these connections with efferents that project to the MPOA-MAH via the dorsal longitudinal fascicle, travelling close to the midline in the periventricular grey matter (Zaborszky and Palkovits, 1978). There is some preliminary evidence that the MPOA-MAH also receives afferents from the central grey via a far lateral route (personal observations). Connections of the MPOA-MAH with the midbrain central grey may be relevant to ultrasonic calling because lesions of the central grey reduce ultrasonic calling in female hamsters (Floody and O'Donohue, 1980). NL and FL cuts may be effective in suppressing ultrasound production because they sever MPOA-MAH/dorsal midbrain connections. Other pathways, however, may be equally relevant. Recently, a fiber system originating from the medial nucleus of the amygdala and travelling ventromedially to the bed nucleus of the stria terminalis has been described by Lehman and Winans (1980). This pathway would have been cut by both NL and FL cuts. Interruption of this pathway in male hamsters reduces or eliminates copulatory behaviour (Lehman and Winans, 1980). Given that olfactory bulbectomy also eliminates male mating behaviour (Murphy and Schneider, 1970), Lehman, Winans, and Powers (1980) argue that olfactory connections with the medial amygdala are important for hamster copulatory behaviour. The medial amygdala, in turn, may relay olfactory information controlling male sexual behaviour to the MPOA-MAH by way of its ventromedial connection with the bed nucleus of the stria terminalis. A similar or identical circuit may also be important for ultrasound production. It has already been established that olfactory bulbectomy can also reduce ultrasonic calling in female hamsters (Kairys, Magalhaes, and Floody, 1980). The effects of discrete damage to the medial amygdala and bed nucleus of the stria terminalis on ultrasonic vocalizations remain to be seen. Such studies should prove useful in determining whether ultrasound production and possibly other proceptive components of female mating behaviour are neurally organized in the same manner as male reproductive behaviour.

Whether or not animals were allowed to hoard food had marked effects on body weight regulation. It should be stressed that Sham-Hoard animals were not food deprived at any point during the experiment. All animals were inspected at least once a day throughout the experiment, and at no point did Sham-Hoard animals run out of food. These animals were given three times the amount of daily food ordinarily consumed by cycling hamsters and nearly twice as much food as ordinarily consumed by lactating animals (Fleming, 1978; Miceli and Malsbury, unpublished manuscript;

Miceli, unpublished data). The only restriction was that these animals were not allowed to construct and maintain a hoard. Yet, the surgical sham and FL hoarders gained more weight from the pre- to postoperative period than respective Sham-Hoard hamsters.

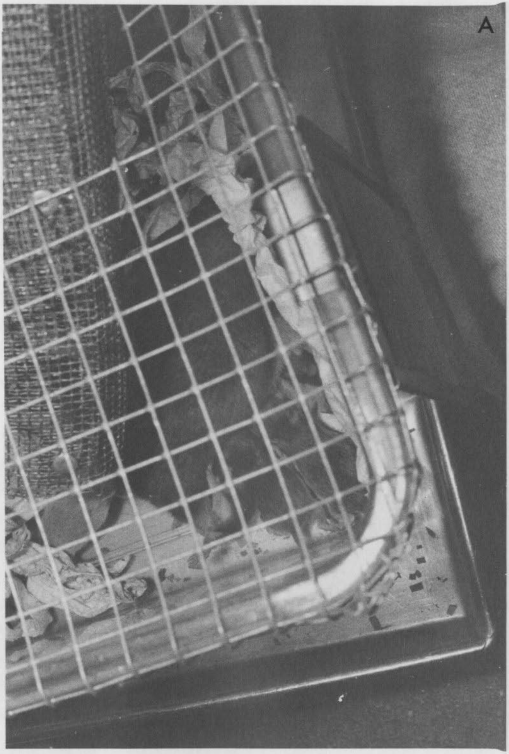
The reason for these body weight differences is not obvious. However, given that hamsters are faced with cyclic periods of food availability and non-availability in their natural habitats (Richards, 1966a), it seems reasonable to assume that hamsters adjust their food intakes and body weights in accordance with either short-term or long-term food availability. This may translate to Sham-Hoard animals reducing their food intake in order to preserve food stores. The reduced body weights of FL and Sham sham-hoarders appear to be regulated because they gained less weight from pre- to postoperative periods, but the weight gains from the postoperative period to parturition were comparable across the groups. Such an interpretation is in agreement with Hainsworth and Wolf's (1979) approach to ingestive behaviour. They call for an integration of ecological and physiological factors to better describe and explain feeding behaviour.

If hamsters do regulate food intake and body weight in accordance with food availability, NL, but not FL cuts disrupted this regulation. FL animals behaved like the surgical shams; those with the hoarding opportunity gained more weight and regulated at higher body weight levels than those without the hoarding opportunity. NL-HD and NL-SH hamsters, on the other hand, did not differ in this respect. This dissociation between NL and FL cuts may be readily explained on the basis of the neuroanatomy of feeding behaviour and body weight regulation. Research on the neural bases of feeding has revealed a longitudinal feeding inhibitory pathway (e.g. Sclafani and Berner, 1977). This longitudinal pathway is situated in the perifornical MFB. Coronal cuts through the perifornical MFB result in hyperphagia and obesity, whereas, coronal cuts placed more medially or laterally do not (Paxinos and Bindra, 1972; 1973; Sclafani and Berner, 1977). These feeding inhibitory fibers turn medially at the level of the MAH (Gold, 1970; Paxinos and Bindra, 1973; Sclafani, 1971). These feeding inhibitory fibers, then, were disrupted by NL cuts but not the FL cuts of this study. While it has been argued that the obesity following such brain manipulations may be due to concomitant changes in endocrine secretions and metabolism (Friedman and Stricker, 1976), hyperphagia does follow damage to the longitudinal feeding inhibitory pathway (e.g. Sclafani and Berner, 1977). If, then, hamsters regulate food intake and body weight to available food resources, suppression of food intake would be required during periods of low food availability. Disruption of feeding inhibitory fibers would then reduce this ability.

NL cuts disrupted nest building much more severely than did FL cuts. In the postoperative prepartum period NL animals did not build nests. During the postpartum period the same animals did build nests that did not differ from surgical shams or FL animals with respect to how finely paper towelling was shredded or how tightly it was packed. However, these nests were deficient because bottoms and sides were not lined with woodchips (see Figure 7). FL animals showed a slight nesting impairment postoperatively. However, it did not persist to the second postoperative (Day 15 gestation) nesting observation.

Previous studies of the MPOA-MAH and maternal behaviour have regarded

Figure 7 Photographs of a nesting area belonging to a dam with NL hypothalamic knife cuts. (a) view of the nesting area from above; (b) view from the bottom. Note the presence of strips of paper towelling, but the absence of woodchips in the nesting area.


A


B

disruptions of nesting activity following damage to this area to reflect a nesting deficit specific to maternal behaviour. The MPOA-MAH, however, is also functionally implicated with autonomic and behavioural thermoregulation (see Satinoff, 1974; 1978 for reviews). Thermal stimulation of the MPOA-MAH elicits both autonomic and behavioural thermoregulatory responses, while destruction of this region only disrupts autonomic thermoregulation (Lipton, 1968; Satinoff and Rutstein, 1970). For example, MPOA lesioned rats become hyperthermic in hot environments but do bar press to turn off a heat lamp and turn on a cooling fan (Lipton, 1968). Hypothalamic knife cuts (similar to NL cuts of this study) along the MPOA-MAH produce similar autonomic effects (Gilbert and Blatties, 1977).

Changes in nesting activity following experimental MPOA-MAH damage may be considered compensatory behavioural thermoregulatory responses due to a concomitant reduction in the ability to make autonomic thermoregulatory responses (Satinoff, 1974). This analysis may not be totally satisfactory because male rats with MPOA lesions show slight nest building impairments even in cool environments (Van Zoeren and Stricker, 1977). Yet, one should not preclude the possibility that lactating rats sustaining lesions of or knife cuts along the MPOA-MAH fail to build nests because of a reduced ability to dissipate heat. In a series of experiments (Leon, Croskerry, and Smith, 1978; Woodside and Leon, 1980; Woodside, Pelchat, and Leon, 1980) it has been demonstrated that intact rats begin a nest bout by occluding a portion of their ventrum, thereby decreasing surface area available for heat loss. When the additional heat load causes the dam's core temperature to rise acutely, the nursing bout is terminated. MPOA-MAH lesioned or knife cut rats do not build nests but do nurse pups (Numan, 1974; Terkel et al., 1979). Such lesioned or cut animals would be expected to have short duration in-nest nursing bouts because these animals have difficulty in dissipating heat. Nursing away from a nest would help to alleviate this problem, because there would be no nesting material to insulate heat. Thus, the lack of nest building in the above mentioned studies may well reflect a compensatory thermoregulatory response allowing the rats more contact with their young, rather than a maternal deficit.

The above explanation is consistent with the observed nesting behaviour of NL hamsters of this study. The postpartum nests built by these animals were located well away from woodchips so that when these animals nursed their young, portions of their ventrum made contact with the cool (relative to the mother-litter huddle) cage floor. Yet, pups were protected by surrounding paper towelling. During the postoperative prepartum period the need for a nest would be obviated in these animals. It is interesting to note that of the three NL animals that did build nests during postoperative testing, two had responded maternally towards foster pups. It should also be mentioned that the discrepancy between the present postpartum nesting data and those of previous studies may be reconciled by differences in the time animals were alloted to build nests before they were rated. While experimental hamsters in this study were given paper towelling three days prior to the rating of nests, Numan (1974) and Marques et al. (1979) only gave their animals one hour between the presentation of paper towelling and the rating of nests. Within the alloted hour their knife cut or lesioned animals did not build nests.

However, Numan (1974) reported that his knife cut rats did build "inferior" nests overnight. He does not mention in what way the nests were inferior.

As in studies of other behaviours, the position and plane of orientation of knife cuts have been varied to reveal thermoregulatory neuropathways. Coronal cuts that sever the connections between the MPOA and MAH do not produce deficits in resistance to overheating and overcooling (Lipton et al., 1974), while long sagittal cuts interrupting most of the lateral MPOA-MAH connections (as do the NL cuts of this study) caused a marked disturbance in autonomic regulation of temperature (Lipton et al., 1974; Gilbert and Blatties, 1977). These independent groups of researchers have concluded that the lateral connections of the MPOA-MAH critical for autonomic thermoregulation descend through the MFB. While core temperatures and other thermoregulatory measures were not taken here, the nesting data support this supposition, because FL cuts, which spare MPOA-MAH connections with the MFB, did not produce the nesting alterations seen in the NL animals.

Food hoarding was not disrupted by either NL or FL cuts. That this was so in NL animals is consistent with Marques et al.'s (1979) results. They also found that their "anterior" cut (comparable to the NL cuts here) animals showed no deficits in hoarding behaviour. In that study postpartum animals were given object hoarding tests (food pellets being among the hoarding objects), with the intent to demonstrate that deficits in pup retrieval following knife cuts were not due to a general deficiency related to the picking up and carrying of objects. In this study, more "naturalistic" food hoarding data were collected because it has been argued that food hoarding is a preparatory maternal behaviour (Miceli and Malsbury, unpublished manuscript) which could conceivably be represented by the same neural circuit as other maternal behaviours.

Whether or not animals were given the opportunity to build and maintain hoards, did, however, have dramatic effects on the nature of the pup directed response. Preoperatively, intact animals with the hoarding opportunity were more likely to have exhibited maternal behaviour than the sham-hoarders. This is consistent with recent data collected in this laboratory. Opportunity to hoard food increases the proportion of virgin hamsters which respond maternally towards foster pups (Miceli and Malsbury, in preparation). These findings will be discussed further below.

The decreased cannibalism and exceptionally large litters among animals in the Sham-HD group confirm and extend recent findings (Miceli and Malsbury, unpublished manuscript). The litter size of Sham-HD hamsters at Day 15 lactation is larger than any other experimental or control group reported in the literature to date (Day and Galef, 1977; Marques, 1976; Marques et al., 1979; Miceli and Malsbury, unpublished manuscript). These findings are of prime practical importance to animal breeders dealing in hamsters wishing to reduce breeding costs by maximizing breeding efforts of individual animals. These findings are also of practical significance to researchers working in the area of maternal behaviour in hamsters. In studies conducted in this laboratory (present study; Miceli and Malsbury, in preparation) non-experimental animals providing foster pups for experimental animals were given abundant food inside the cage for hoarding. As a result, few of the foster pups for use in experiments were cannibalized by their own mothers. Therefore, in cross-fostering experiments, time and costs can be reduced because fewer donor dams are necessary.

It has been proposed that in intact lactating hamsters, postpartum cannibalism serves a function of regulating litter size to the availability of both mother's milk and solid food stores (i.e., the hoard) (Miceli and Malsbury, unpublished manuscript). Data collected in this experiment, in addition to extending this finding, also suggest that food-based litter size regulation may occur <u>prior</u> to parturition. In this study, Hoard group hamsters gave birth to more pups than sham-hoarders. For example, mean litter size at parturition for the Sham-HD group was 17.4 pups, and for the Sham-SH group, 13.2 pups. This difference is significant despite the small sample sizes because the largest litter in the Sham-SH group (16 pups) was only slightly larger than the smallest litter in the Sham-HD group (14 pups). On the evening of parturition most animals were checked at ten minute intervals until the end of parturition was determined. The possibility that undetected differential cannibalism between the checks might account for the initial litter size differences between the hoarders and sham-hoarders was not ignored. However, observations of pre- and postpartum cannibalism during the tests suggest that cannibals can not consume an entire pup within eight or 10 min. At the 10 min checks, cages were carefully checked and animals had their cheek pouches examined for hidden pups or pup cadavers. Portions of pups were, in fact, found during these checks indicating that cannibalism was prevalent during and shortly after parturition. However, it is maintained that animals could not have consumed an entire pup within 10 min.

The data then suggest that there were prepartum differences in litter size between hoarders and sham-hoarders. The mechanism underlying such a regulation is difficult to evaluate because these results were rather unexpected and the experiment was not designed to deal with this issue. It remains possible that the available hoard may have induced more ova to be released during ovulation, or it may have enhanced implantation. Alternatively, resorption or abortion may have gone by undetected in sham-hoarders during gestation. This finding warrants further investigation.

The effects of the knife cuts on virgin and postpartum maternal responsiveness are complex. The NL cuts of this study are comparable to Marques et al.'s (1979) "anterior" cuts. Moreover, the NL-SH group here is functionally similar to Marques et al.'s anterior group because those animals were not housed in a manner which would allow food hoarding. In the postoperative prepartum tests, the effects of the knife cuts in the NL-SH animals are clear. The cuts had converted those hamsters having met the criterion for maternal behaviour preoperatively into cannibals. Marques et al. (1979) found similar results with their anterior cuts. In the present study, NL cuts were not as effective when the animals were allowed to hoard. Two of the eight NL-HD animals were resistant to the disruptive effects of the cuts; that is, they remained maternal postoperatively. Their cuts were no different from those of animals in the same group that had been converted into cannibals.

During the postpartum period NL animals showed dramatic changes in maternal responsiveness. These animals built nests, sniffed, licked, nursed, and all but one of the 14 retrieved pups. Marques et al. (1979)

also found that some of their anterior cut animals which cannibalized as postoperative virgins retrieved pups during postpartum tests, but the improvement in that study was not nearly as dramatic as observed here. These results contrast with results of rat experiments. As mentioned earlier, rats with MPOA-MAH lesions (Numan, 1974; Jacobson et al., 1980) or with parasagittal knife cuts along this continuum (Numan, 1974; Smotherman et al., 1977; Terkel et al., 1979) sniff, lick, and nurse pups, but do not build nests or retrieve pups. In rats, the apparent inability to initiate nest building and pup retrieval following the above mentioned brain manipulations may be described as a motivational deficit. Hamsters do not show a deficit as such following the same surgical procedures. The hamster deficit is more difficult to characterize.

Evaluation and interpretation of the present data is a difficult task because presently there is no firmly established theoretical framework in which to study hamster maternal behaviour; that is, a baseline of "normal maternal behaviour" with which the effects of the cuts could be compared is not available. Other investigators have overcome this problem by assuming the same theoretical framework of maternal behaviour provided for the rat in the hamster (e.g., Siegel and Rosenblatt, 1980). Therefore, it is not uncommon to see terms such as "sensitization" (Swanson and Campbell, 1979b) or "maternal induction" (Buntin, Jaffe, and Lisk, 1979) describing the appearance of maternal behaviour in female hamsters. These terms are borrowed from the rat literature (e.g., see Rosenblatt et al., 1979) and may not accurately describe what is actually occurring in hamsters. The appearance of maternal behaviour in the hamster may be better described as the offset of cannibalistic behaviour. In heuristic terms, the appearance of maternal behaviour in hamsters may represent the "turning off" of cannibalistic behaviour rather than the "turning on" of maternal behaviour. This distinction is not merely semantic. The underlying implication is that the neural substrate for maternal behaviour is spontaneously active, or that it is under the inhibition of a cannibalistic substrate. There is experimental evidence to buttress the behavioural end of this argument. A fair proportion of virgin hamsters, up to 50%, are spontaneously maternal towards foster pups (Marques and Valenstein, 1976). Those virgin animals not showing maternal behaviour during initial contact with foster young show the opposing response, cannibalism, and only a small percentage of animals are indifferent towards test pups (Marques and Valenstein, 1976; Miceli and Malsbury, in preparation; Rowell, 1960; present study). Moreover, virgin hamsters need very few days of pup presentations before showing the maternal response (Siegel and Rosenblatt, 1978; Swanson and Campbell, 1979b); those that initially cannibalize will later show maternal behaviour (Buntin et al., 1979; Miceli and Malsbury, in preparation; present study). Also, the transition from cannibalistic to maternal behaviour is normally direct and not mediated by a period of indifference towards pups (Miceli and Malsbury, in preparation). These studies illustrate the fact that intact hamsters will show one response but not the other and are interpreted to mean that maternal behaviour can only be expressed when cannibalistic behaviour is suppressed.

It is proposed that NL (and FL) cuts disrupted part of a neural system underlying the inhibition or suppression of pup cannibalism, rather than a maternal activating system. The behavioural consequences of such cuts can be best described as a failure to inhibit cannibalistic responses. The behaviour of two NL animals during the postpartum tests illustrate this point. These animals approached, sniffed, and retrieved pups back to the nest. At the nest, sniffing and licking of pups continued, and at some point shortly after, one or more pups were eaten. As can be seen by the declining litter sizes in knife cut groups throughout lactation, this pattern of behaviour can be generalized to other knife cut animals. This behavioural effect can not be attributed to a failure to tend to cues that ordinarily act to suppress cannibalism because knife cut animals, given the opportunity, hoarded food and reared larger litters than their counterparts given daily food rations. In fact, these animals reared larger litters than surgically intact sham-hoarders, and larger litters than intact animals in other studies (e.g. Day and Galef, 1977; Marques, 1976).

The pre- and postpartum maternal behaviour of FL groups did not differ from corresponding NL groups, suggesting that these two types of cuts severed a common pathway important for maternal behaviour. This contention is substantiated by the behaviour of animals with the mediolaterally asymmetrical cuts. Essentially, the maternal behaviour of ASYM animals did not differ from either NL or FL animals. Three of the four ASYM animals were from hoarding groups. Two of these animals had completely cannibalized their litter early in the postpartum period. The other two animals successfully reared moderate sized litters (four and 12 pups) to the end of the postpartum period. During the postpartum tests, three of these animals consistently showed pup retrieval, while the other animal consistently cannibalized pups after having retrieved them. This syndrome is characteristic of that produced by bilateral NL or FL cuts.

As with ultrasonic calling, the rostrocaudal position of knife cuts effectively altering normal maternal patterns was at the level of the suprachiasmatic nucleus. Cuts extending further rostrally into the MPOA did not produce behavioural effects that were observably different from those produced by cuts beginning further caudal. These results are consistent with Marques et al.'s (1979) finding with the hamster, but not with recent rat findings. Using the knife cut (Terkel et al., 1979) and lesion (Jacobson et al., 1980) techniques in rats, these workers report that the critical lateral fiber connection underlying maternal behaviour is confined to a narrow band of tissue situated in the caudal MPOA just beneath the anterior commissure. Lesions sparing, or cuts beginning caudal to this tissue did not disrupt rat maternal behaviour. At this point it is not clear whether these differences represent species differences in neural control of maternal behaviour, or whether fibers coursing laterally at the level of the hamster anterior hypothalamus originate at or travel to the MPOA.

FL cuts, which spare connections of the MPOA-MAH with the MFB, were just as effective as NL cuts in producing disruptions in normal maternal processes. This finding suggests that the mediolateral connections of the MPOA-MAH, other than with the MFB, are important for this behaviour. Since both FL and NL cuts severed axons travelling in the region of the SOC, it is proposed that SOC connections, rostral to those important for sexual receptivity (Malsbury et al., 1979), may also be critical for maternal behaviour. While these data refine our ideas about the neural pathways mediating maternal behaviour, the source and/or projection field of supraoptic axons important for maternal behaviour remain to be defined. The present data indicate that NL and FL cuts along the MPOA-MAH do not alter motivated aspects of maternal behaviour in the hamster. Instead, a relatively simpler concept is proposed to define the behavioural consequences of these cuts, that of a failure to inhibit pup cannibalism. If such is the case, amygdalar-hypothalamic connections may be relevant.

In virgin rats, lesions of the corticomedial nucleus of the amygdala result in a shortened latency to maternal behaviour (Fleming et al., 1980). These workers have interpreted these findings to mean that this nucleus relays inhibitory olfactory information to the MPOA-MAH, via its major efferent, the stria terminalis. At a behavioural level, this circuit is assumed to suppress maternal responsiveness in intact virgin animals and its disconnection by either olfactory damage (Fleming et al., 1979), corticomedial amygdaloid or stria terminalis lesions (Fleming et al., 1980), releases the MPOA-MAH from this inhibition as evidenced by rapid onsets of maternal behaviour.

The amygdala is also functionally implicated with various components of aggressive and predatory behaviours (see Karli, Vergnes, Eclancher, Schmitt, and Chaurant, 1972; Karli, Vergnes, Eclancher, and Penot, 1977). Specifically, it is believed that certain amygdaloid nuclei and their efferents may mediate the suppression of such behaviours. Lesions of the corticomedial amygdala, stria terminalis, and bed nucleus of the stria terminalis have been found to enhance muricide in rats (Albert and Brayley, 1978; Vergnes, 1976). Conversely, activation of a proposed serotonergic system in the corticomedial amygdala by intracerebral serotonin injections decreased shock-induced attacks towards conspecifics in rats (Rodgers, 1977). Pup cannibalism by female hamsters is similar to predatory behaviours in several respects. For example, an appetitive phase (the attack and killing of pups) usually precedes a consummatory phase (ingestion of attacked pups) in a cannibalistic encounter (personal observations). It should, however, be kept in mind that despite the apparent similarity of pup cannibalism to predatory behaviour, it may be a separate behavioural entity, with a separate representation in the central nervous system. Marques' (1979) finding that damage to the olfactory systems will produce profound alterations in maternal responsiveness while leaving predatory behaviour (cricket killing) unaffected in the hamster illustrates this point. Yet, the possibility of amygdaloid involvement in the inhibition of pup cannibalism should not be ignored.

Several speculations can be made as to the possible amygdalar-hypothalamic pathways underlying the suppression of pup cannibalism. MPOA-MAH axons travelling through the SOC project to several amygdaloid nuclei, the medial amygdala receiving the heaviest projection (Conrad and Pfaff, 1976a; 1976b). These fibers may ordinarily act to alter neurons in the amygdala associated with various aggressive and predatory behaviours (Karli et al., 1977). Alternatively, NL and FL cuts may have interrupted the ventral amygdalo-fugal pathway connecting amygdaloid nuclei and the hypothalamus (De Olmos, 1972; Lammers, 1972). While these workers have questioned whether such a pathway originates from the amygdala proper in rodents, the combination of horseradish peroxidase histochemistry with behavioural testing has led to the discovery of a ventral pathway from the medial nucleus of the amygdala to the bed nucleus of the stria terminalis essential for copulatory behaviour in the male hamster (Lehman and Winans, 1980). In addition to ultrasonic vocalizations, this pathway may also be relevant to maternal processes in the female hamster.

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