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Olfactory processing of spatial information in hamsters

Tomlinson, William Thomas, Jr., Ph.D.

The University of North Carolina at Greensboro, 1989

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OLFACTORY PROCESSING OF SPATIAL INFORMATION IN HAMSTERS

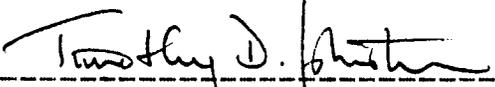
by

William Thomas Tomlinson, Jr.

A Dissertation Submitted to
the Faculty of the Graduate School at
The University of North Carolina at Greensboro
in Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

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1989

Approved by



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APPROVAL PAGE

This dissertation has been approved by the following committee of the Faculty of the Graduate School at the University of North Carolina at Greensboro.

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The purpose of this research was to elucidate the nature and ontogeny of spatial information processing in hamsters. The study consisted of a series of spatial tasks administered to hamsters reared under different conditions.

Experiment 1 demonstrated that hamsters reared on solid food, but not hamsters reared on a liquid diet, increased their exploratory behavior after a change in the spatial location of two odor cues when forced to adopt an allocentric frame of reference. Experiment 2 showed that liquid-reared hamsters could detect a change in the spatial location of odor cues if allowed to adopt an egocentric frame of reference.

Experiment 3 showed that the liquid-reared hamsters could detect a change in the spatial location of two visual cues when forced to adopt an allocentric frame of reference. Experiment 4 compared a group of hamsters which experienced restricted exploratory experiences early in development with the liquid-reared and normally-reared animals tested in Experiment 1. A series of orthogonal comparisons indicated that the normally-reared group differed from both experimental groups. The restricted-rearing group and the liquid-rearing group did not differ and both failed to detect a change in the spatial location of odor cues from an allocentric frame of reference.

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CHAPTER 1

Introduction and Background

"The spatial concepts of distance and direction seem to me of the very warp and woof of all our thinking about performances whether these performances involve actual space or mere mechanics or mere logic" (Tolman, 1959).

Ever since Small (1900) introduced the modified Hampton Court maze to American psychologists, studies of spatial memory have played an important role in psychology (see Olton, 1979, for a review). Tasks requiring animals to remember the spatial features of a familiar space have been used to study working memory (Olton & Samuelson, 1976), cognitive maps (Tolman, Ritchie, & Kalish, 1946; Menzel, 1973, 1978; Poucet, Chapuis, Durup, & Thinus-Blanc, 1986; Chapuis & Thinus-Blanc, 1987), foraging strategies (Olton & Schlosberg, 1978), and the underlying anatomical (O'Keefe & Nadel, 1978; Haaren, Zijderfeld, van Hest, de Bruin, van Eden, & van de Poll, 1988; Rudy & Sutherland, 1989) and neurochemical substrates of memory (Bostock, Gallagher, & King, 1988). Ethological research (e.g., Hoffman, 1985; Kamil, 1978; Jamon & Bovet, 1987; Moore & Phillips, 1988) has demonstrated impressive spatial capabilities among a wide range of species, and laboratory studies have provided an understanding of the mechanisms of spatial processing used by animals under natural circumstances.

Characteristics of Spatial Information Processing

Spatial processing involves the acquisition, storage, and retrieval of spatial information. Acquisition consists of the behavioral and sensory capabilities that allow the animal to gain spatial information from the environment. Storage processes concern the encoding of spatial information and theories of information storage often hypothesize specific neural locations for stored experiences (see discussion below). Retrieval involves the behavioral, sensory, and cognitive capabilities that allow the animal to use its stored experiences. These three activities play critical and interconnected roles in spatial processing.

Exploratory behavior plays a particularly important role in the acquisition of spatial information (Maier, 1932; Ellen, Parko, Wages, Doherty, & Herrmann, 1982; Chapuis, Durup, & Thinus-Blanc, 1987). For example, rats require considerable exploratory experience before taking the shortcut in Maier's (1932) "three-table problem" (Ellen, et al., 1982). Exploratory behavior consists of behaviors which make available to the animal perceptions of its environment (McReynolds, 1962). McReynolds (1962) has proposed that "animals develop a cognitive structure which represents for them the nature of the world" (p. 312). This cognitive structure, or schema, provides a reference guide against which new perceptual information can be compared (Neisser, 1976). When the animal encounters novel stimuli, exploratory behavior provides a mechanism by which new perceptual features of the stimuli can be integrated into existing schemata. Therefore, when faced with an unfamiliar space, or a novel arrangement of objects in a familiar space,

exploratory behavior permits the acquisition of new information. Thus, one function of exploratory behavior is to acquire new spatial maps or to update existing maps (Tolman, 1948; O'Keefe & Nadel, 1978).

Acquisition of spatial information can occur through any of several sensory modalities, different species relying on different modalities. For example, the desert isopod Hemilepistus reaumuri uses tactile cues, received via the antennae and provided by an embankment built from its feces (the fecal ring), to orient towards its burrow entrance (Hoffmann, 1985). The insect acquires information about the location of an important goal, the burrow entrance, by use of tactile cues provided by this distinctive landmark. Jamon, Benhamou and Sauve (1986) have suggested that wood mice (Apodemus sylvaticus) may gain spatial information from odor cues provided by aromatic plant species. In their study, mice captured and released 120 or 250 meters from their home range tended to orient along a familiar vegetation gradient (p. 54). These results suggest that the mice acquire spatial information provided by the odor cues in their environment.

Of course, the visual modality provides spatial information for many species. Vander Wall (1982) provided Clark's nutcrackers (Nucifraga columbiana) with the opportunity to cache seeds in an oval test space containing distinctive visual landmarks. Prior to a subsequent search session, during which the birds were allowed to recover their hidden seeds, the distinctive visual landmarks in the space were shifted. During recovery of seeds the birds made searching errors in the direction of the shift in visual cues. These results indicate that visual cues provide spatial information to Clark's

nutcrackers and memory for those cues guides later search behavior (see also Kamil & Balda, 1985).

Encoding or storage is the second important component of spatial processing. Generally encoding involves the storage of an experience in some retrievable form. This review does not address the storage theories from human cognitive work, primarily because those theories tend to be related to species-specific characteristics of human memory (Tulving, 1982; Cohen & Squire, 1984; Squire, 1987; Milner, 1970). Storage theories based on animal models abound (O'Keefe & Nadel, 1978; Olton, Becker, & Handelmann, 1979; Mishkin, Malamut, & Bachevalier, 1984; Sutherland & Rudy, 1989) and provide insight into different types of encoding and their prospective storage sites, as well as the nature of the stored experience. The hippocampus has been identified as a neural region necessary for successful completion of most spatial tasks (O'Keefe & Nadel, 1979; Olton & Papas, 1979; Rudy & Sutherland, 1989), suggesting that it is the site for storage of spatial information. Although the nature and organization of stored spatial information cannot be directly assessed, analysis of an animal's behavior during retrieval does allow one to make inferences about the nature of the encoding process and the encoded information.

The Nature of Stored Spatial Information

O'Keefe and Nadel (1978, 1979) provide one theoretical account of the nature of spatial representations in which animals acquire a map-like representation of their environment. The map consists of "a set of place representations connected together according to the rules which represent distances and directions amongst them" (O'Keefe & Nadel, 1979,

p.488). Their conclusions were reached on the basis of research done with various place learning tasks, such as the radial-arm maze. Place-learning tasks involve a goal that is in a fixed location in relation to perceivable and discriminable features of the environment but that is not specified by any single clue. O'Keefe and Nadel (1978) believe that attaining the goal in such tasks requires the animal to remember the map-like features of the space. Menzel's (1973, 1978) work demonstrates the use of spatial maps in chimpanzees and provides support for the spatial-mapping hypothesis of O'Keefe and Nadel (1978). Menzel (1973) had chimps carried around a familiar compound while food was hidden in 18 places. The chimps observed each piece of food being hidden. The path taken was tortuous and crossed itself several times. After the food was hidden the chimp was released and allowed to hunt for food. The chimps recovered about 12 of the 18 pieces of food and typically did so by taking a large circular route through the compound. These results suggest that the chimps remembered the geographic locations (rather than the sequential positions) of the food and their memory for those locations helped organize their search behavior into an efficient pattern.

Sutherland and Rudy (1989) provide a similar but more flexible account of memory processes used in place-learning tasks. In their account, a configural association system (CAS) operates in parallel with a simple association system (SAS). The SAS "records organism's experiences as changes in the strength of associations between elementary stimulus units" (p. 129) while the CAS "combines the representations of elementary stimulus events to construct unique

representations and allows for the formation of associations between these configural representations and other elementary representations" (p. 129). Their account of the associative strength of a stimulus follows that of Spence (1936) in which the strength of a stimulus compound is the sum of the strengths of the combined stimuli. Although they view the systems as operating in parallel they believe the two systems to be served by different neural substrates: the CAS relies on the hippocampal formation but the SAS does not.

In Sutherland and Rudy's (1989) theory, spatial tasks requiring place learning can only be solved by use of the CAS. The Morris water maze (Morris, 1981) provides an example of a task requiring the use of the CAS. A rat is placed on a raised platform located in a circular pool of opaque water and allowed to visually inspect the cues around the pool. After the rat views the features of the space it is returned to a holding cage and the platform is lowered below the surface of the water. The rat is then placed in the pool of water and is required to locate the hidden platform. The platform always remains in the same location relative to the cues outside of the pool. Rats quickly learn to navigate to the hidden platform regardless of their starting position. The task requires use of the CAS because the animal must create and store configurational information about the visual features of the environment as seen from specific locations in the pool.

Laboratory studies have greatly increased our understanding of spatial processes but ethological studies have also contributed by providing examples of spatial processing in a wide range of species and circumstances. Orientation during large-scale migratory movements

provides perhaps the most impressive demonstration of spatial capabilities (Baker, 1978), but orientation on a smaller scale has also been investigated (see the earlier discussion of Hoffman's [1985] and Vander Wall's [1982] research). Spatial processing is important for orienting, foraging, and homing towards a nest or territory and generally animals are quite proficient at remembering the spatial properties of a familiar environment. For example, Kamil (1978) provided evidence that Hawaiian honeycreepers (Loxops virens) use spatial memory during foraging. He reported that honeycreepers do not return to a flower for several hours after having fed on it, thus allowing the for the flower's nectar supply to be replenished. They did not use a response chaining strategy (such as starting at one end and flying in a straight line away from the starting point) and they made no perceptible changes in the flower itself. Apparently the birds are able to avoid the flowers they have recently visited by remembering the location of those flowers. Jamon and Bovet's (1987) study described above demonstrated that mice are quite proficient at using memory for the location of vegetative cues for orienting towards their home range.

The Dishabituation Paradigm in the Study of Spatial Memory

One experimental paradigm that has proven especially valuable for the study of spatial memory in animals involves the use of habituation-dishabituation processes. The habituation-dishabituation procedure relies on the test animal producing an exploratory or orienting response (Pavlov, 1927; Sokolov, 1963) to the presence of a novel stimulus. The orienting response diminishes in intensity with repeated presentations of the stimulus and with continued presentations the orienting response

will decline to an undetectable level. This reduction in the orienting reflex is called habituation (Harris, 1943; Stephenson & Siddle, 1983). After the orienting response is habituated, introduction of another stimulus, different from the first, will produce a reappearance of the response. The reappearance of the orienting response is called dishabituation.

Generally, habituation-dishabituation studies proceed as follows. The subject is presented with a stimulus such as an object, a particular spatial layout, or a group of objects. Initially the subject will direct high levels of an exploratory behavior such as looking or touching towards the stimulus (see below); however, after repeated presentations the exploratory behavior diminishes or habituates. After habituation a change is made in some aspect of the stimulus, after which the animal's exploratory behavior may increase, or dishabituate. Such dishabituation of exploratory behavior indicates that the subject detected the change in the stimulus, which implies that it had some representation of the initial stimulus with which to compare the new stimulus. This paradigm has been used to test memory for many different stimulus properties with a host of species.

Habituation is distinguished from sensory adaptation, such as occurs with differential bleaching of color pigments in the retina (Cornsweet, 1970), in at least two ways. First, sensory adaptation can be directly traced to changes in the receptor cells of the sensory apparatus whereas habituation cannot. Second, habituation applies to situations involving more complex stimuli, usually requiring higher brain centers for their discrimination. When dealing with more complex

patterns habituation appears to be an index of the creation of an internal representation of the stimulus event (Bower & Hilgard, 1981).

The orienting reflex and exploratory behavior both provide the animal with perceptual information about its world (Sokolov, 1963; McReynolds, 1962). In many respects the orienting reflex and exploratory behavior function in the same way, since both transform novel stimuli into familiar stimuli. Both deliver information to the animal for comparison with memory for other experiences. We can conclude that the incoming information is compared to some stored experience because of the way stimuli are differentially explored based on previous experience with the stimuli: familiar stimuli elicit less exploratory behavior than do novel stimuli.

Habituation-dishabituation paradigms have advanced our understanding of memory in human infants (Meltzoff & Borton, 1979) and in animals (Thinus-Blanc & Ingle, 1985; Poucet, et al., 1986). Meltzoff and Borton (1979) presented infants with objects and allowed them to become familiar with the object by oral manipulation. After becoming familiar with the objects, after mouthing of the object habituated, the infants were presented with visual forms of either the familiar objects or novel objects. Infants presented with familiar objects spent less time looking at (visually exploring) the object than those presented with novel objects. Meltzoff and Borton (1979) concluded that infants remember the amodal features of a stimulus since exploration dishabituated more to novel than to familiar stimuli, suggesting that there was new information to be gained from the new stimulus.

Researchers have used the dishabituation of exploratory behavior in open-field tasks to examine spatial memory in gerbils (Thinus-Blanc & Ingle, 1985) and hamsters (Poucet, et al., 1986). Thinus-Blanc and Ingle (1985) allowed gerbils to explore the interior of a rectangular cardboard arena which had white walls, a white translucent roof, and five black stripes on one wall. After familiarization with the test space the animals were reintroduced into the arena which now contained a Magic Marker pen or a D-size flashlight battery. The gerbils' exploratory behavior directed at the object, defined as contacting the object with their snout, declined over a series of one-minute trials. After five such trials the experimenters moved the object to a new location. The gerbils returned to the box through a door not used in the initial five trials and were allowed to explore. All gerbils in this study exhibited increased levels of exploration in the sixth trial, the trial with a new spatial arrangement. Thinus-Blanc and Ingle (1985) concluded that the gerbils processed the spatial features of the test arena during the first five trials and were able to detect a change in the spatial location of the object on the sixth trial.

Poucet et al. (1986) demonstrated that hamsters remember the spatial locations of several objects in a spatial array. Hamsters were placed in a familiar arena containing four objects in a particular spatial arrangement. The hamsters exhibited a high level of exploration, as measured both by the number of contacts with the objects and by time in contact with the objects, during the first of three sessions. During the second session the hamsters reduced their level of exploration (habituated). After the second session the objects were

rearranged and the hamsters reintroduced into the arena. In session 3 the hamsters exhibited increased levels of exploration. The dishabituation of exploratory behavior indicated that the animals perceived the spatial change and allows us to infer that the animal processed the initial spatial arrangement and had some way of comparing the new array to the old one (that is, it had acquired, stored, and retrieved information about the initial spatial layout). Furthermore, Poucet et al. (1986) demonstrated that the knowledge of the previous layout organized exploration of the new arrangement. Only the objects in the array that had been moved were the focus of increased exploration; in other words, a spatial change in some of the stimuli did not result in overall increased levels of exploration.

These studies have greatly increased our knowledge of the cognitive abilities of rodents; however, they do raise several important questions. The first question concerns the nature of the spatial knowledge possessed by the subjects. Do the animals possess configurational memories or could a more simple associative memory have been used to detect the spatial change? Animals can orient in an environment by adopting an allocentric (abstract) frame of reference or an egocentric (body-oriented) frame of reference (Pick & Lockman, 1981). These distinctions are related to the distinction between place learning (allocentric frame of reference) and response learning (egocentric frame of reference) made by Tolman (Tolman, Ritchie, & Kalish, 1947). In order to detect a spatial change from an allocentric frame of reference the animal must remember configurational properties of the environment; that is, it must remember how the spatial locations of the objects are

related to each other and to various stationary components of the test space. To detect a change from an egocentric frame of reference only requires that the animal remember the location of objects in relation to its own body; thus, detecting a spatial change from an egocentric frame of reference can be done by recalling a more simple spatial relationship or association than does adopting an allocentric frame of reference.

The animals in Poucet et al.'s (1986) study always entered the arena from the same location and so might have detected the changes in the positions of the objects by adopting an egocentric frame of reference, remembering the location of the objects relative to their body coordinates at the starting point. Although this is a type of spatial responding it does not require the formation of configurational associations (Sutherland & Rudy, 1989; discussed above) that detecting the change from an allocentric frame of reference requires. Controlling the animals' frame of reference during the task would allow for more specific inferences concerning the type of spatial knowledge possessed by the hamster. For example, if the hamsters in Poucet et al.'s (1986) study were forced to adopt an allocentric frame of reference, and they then showed evidence of remembering the spatial location of the objects, we could infer that they possessed memory for the configurational layout of the test space.

A second question raised by these and other laboratory studies of spatial processing concerns the modality used to deliver spatial information to the animals. Typically spatial studies have focused on the processing of spatial information from visual cues; the animals were required to detect a spatial change in one or more visually conspicuous

objects. However, most rodents possess well-developed olfactory systems, suggesting that olfactory mapping of the environment may be important in their spatial behavior. For example, hamsters are known to use olfaction to guide early exploratory forays from the nest (Schoenfeld & Leonard, 1985) and as adults use odor cues to recognize members of their own species (Murphy, 1977). Murphy (1977) allowed females of three different species to approach any one of three males, each of a different species, and found that females approached conspecific males with greater frequency than males of other species. Hamsters also recognize individuals on the basis of odor cues (Johnston, 1983; Johnston & Rasmussen, 1984). Male hamsters that have mated to satiation are rearoused when placed with a new female. It appears that this discrimination is made on the basis of differences in the odors produced by the female's flank glands. Odor cues play an important role in the behavior of adult hamsters and so it is reasonable to ask whether hamsters can remember configurational associations involving olfactory stimuli.

In an effort to address the questions raised above, Tomlinson and Johnston (in preparation) followed a procedure very similar that used by Poucet et al. (1986) with the following exceptions. Adult hamsters were allowed to explore an empty circular arena for 15 minutes. Hamsters entered the arena from the west. A striped pattern was positioned 22 cm above the arena floor on the eastern arena wall and the arena was lit by a 60-watt light bulb located 124 cm above the arena floor. There were no other distinctive visual cues outside of the arena. After this familiarization period and a subsequent 15-minute rest period the

hamsters were again placed into the west end of the arena which now contained two identical visual cues (cheese shakers) each possessing a distinctive odor (honeysuckle or gardenia). The number of contacts and time in contact with the cheese shakers served as a measure of exploratory behavior. As expected, the hamsters exhibited high levels of exploration in this first session, after which hamsters were given a 10-minute rest period. In a second session, hamsters, again entering the arena from the east, displayed reduced exploration of the objects. After this habituation of exploratory behavior the spatial location of the objects were switched, effectively changing only the location of the odor cues. In the critical third session animals were returned to the arena, again from the east side of the arena, and allowed to explore the new spatial arrangement of the odors. Hamsters tested under these conditions increased their level of exploration during session three.

These results suggest that hamsters can remember spatial information derived from olfactory cues. However, this task could have been solved using either simple or configurational associations; that is, the animals could have adopted either an egocentric or an allocentric frame of reference, because they entered the arena from the same direction on all three trials. Thus, in a subsequent experiment hamsters entered the arena from a new direction on the critical third trial which forced them to adopt an allocentric frame of reference to detect the spatial change. Again hamsters dishabituated during the third session. Because of the change in starting point for session three we were able to conclude that hamsters do remember the configurational properties of olfactory cues within a familiar space.

Contribution of Experience to the Development of Spatial Processing

It should not be surprising that hamsters are able to remember the spatial location of olfactory cues given their developmental history. Hamster pups can detect odors as early as postnatal days 3 to 4 (P3-4; Crandall & Leonard, 1979) and actually use olfaction to guide nipple attachment at birth (Teicher & Blass, 1977). Leonard (1975) and others (Schwob & Price, 1978; Westrum, 1975) have identified a number of rudimentary olfactory circuits in the brain of newborn hamster pups. Although the simple task of detection occurs early in development, it is not until P7-8 that pups are able to demonstrate a preference for odor cues (Schoenfeld & Leonard, 1985). By P7-8 hamster pups show a preference for nest odors independent of their preference for warmth (Crandall & Leonard, 1979). This is important because it indicates the decline of behavioral control by thermal mechanisms that link hamsters to their nest early in development (the "thermal tether") and an increase in control of behavior by the the olfactory system. Between P7 and P12 hamsters still are unable to search for and consume solid food and so must be able to return to the nest for suckling (Schoenfeld & Leonard, 1985). It is at this time that the "olfactory tether" develops and helps protect the pup from inadequate retrieval by the mother. During the period P8-12, the olfactory system assumes progressively more control of the hamsters' behavior.

An increase in exploratory behavior out of the nest occurring around P12 may reflect an increased responsiveness to non-nest odors (Schoenfeld & Leonard, 1985). In one study (Schoenfeld & Leonard, 1982) litters (7 to 8 pups) ages P3-P18 were placed into a test cage

containing either partially soiled, fresh, or lemon-scented pine shavings. Locomotor behavior differed as a function of age and odor conditions. When placed in partially soiled pine shavings the pups took two to three minutes to huddle regardless of age. Pups P3-P11 took the same amount of time to huddle regardless of the odor substrate. However, pups P12 or older took longer to regroup when placed in a substrate containing a novel odor. The authors conclude that odor cues gain more relevance for the hamster after P12. A surge in sniffing also occurs by P12 and reaches a maximum by P14. This surge in sniffing may be related to the increase in exploratory behavior. Johnston and Coplin (1979) found that hamsters spent more time sniffing at test odorants on a glass slide at P14 than at P7, P10, P17, or P20. Their results suggest that eye opening, which usually occurs late on P14, reduces odor-induced sniffing. The decline may occur because of new competing stimuli delivered by the visual system.

Studies comparing memory for rodents of different ages abound (Kail & Spear, 1984); however, the number of studies examining the impact of early experience on subsequent spatial processing in rodents are limited (e.g., Cramer, et al., 1988; Castro & Rudy, 1987). One study examining early experiential effects on later spatial processing (Cramer et al., 1988) found that rat pups reared with access to few nipples rarely shift from nipple to nipple during suckling whereas rats reared with access to many nipples do so frequently. Furthermore, they showed that rat pups that nipple-shift frequently reach criterion on an 8-arm radial arm maze faster than do pups which did not nipple-shift. The researchers suggest that pups who frequently nipple shift may adopt

the win-shift strategy needed to learn the maze more easily than pups with limited nipple-shifting experiences. Rats predisposed to learn a win-shift strategy will also be predisposed to perform successfully in a radial-arm maze because after gaining food in one runway they will be unlikely to enter that arm again. Thus this study showed that an early experience, nipple-shifting, plays an important role in adult spatial behavior in the radial-arm maze.

Castro and Rudy (1987) examined the effects of early-life malnutrition on the performance of different aged rats in two versions of the Morris (1981) water-maze task. Pups in the malnourished rearing group spent 12 hours of each day with a lactating female while control animals spent 24 hours a day with a lactating female. This feeding regimen was carried out for 16 days while other factors such as handling and maternal care were equated. Pups were then tested on one of two versions of the Morris water-maze task. The distal-cue version of the task required the animals to remember the configural arrangement of distinctive visual features outside the maze to find a hidden, submerged platform (Morris, 1981; see description above). In the proximal-cue task, the escape platform was visible and the animals could swim directly towards it. The distal-cue task requires configural memory for successful completion whereas the proximal-cue task requires only a simple association between the visual cue of the platform and escape from the pool. Malnourished animals failed to locate the platform in the distal-cue but not the proximal-cue task, whereas normally-reared animals located the platform in both tasks. Since early-life malnutrition has been linked to a permanent decrease in hippocampal DNA

content (Fish & Winick, 1968; Patel, 1983) and a reduced number of hippocampal cells (Jordan, Howells, McNaughton, & Heatli, 1982), Castro and Rudy (1987) argue that hippocampal regions provide the underlying neural substrate for configural memory. Their study, in conjunction with other lesioning (O'Keefe & Nadel, 1979; Olton & Papas, 1979; Rudy & Sutherland, 1989) and pharmacological (Bostock, Gallagher, & King, 1988) studies, suggests that impairment of distal-task performance occurs as a result of damage to the hippocampus resulting in this case from malnutrition.

A pilot study conducted in our lab raised several interesting questions concerning the role of early experience in later spatial processing. The pilot work involved testing two litters of four animals each raised under different conditions in procedures developed by Tomlinson and Johnston (in preparation; see details above). The two litters were raised on different diets; however, all other physical aspects of the rearing situation (such as bedding, nesting material, water, and lighting) were the same. One litter was raised under standard lab conditions receiving rodent chow ad libitum while the other litter was reared on a liquid diet of Kitten Milk Replacement (Borden). The pups were tested on P28 for their ability to remember the spatial relationships among olfactory cues. Testing was conducted under conditions requiring the use of an allocentric strategy as described above. Normally reared pups increased their exploration during the critical third session. This dishabituation was taken to mean that the hamsters recognized the change in the spatial configuration of the odor cues and confirmed the results of the earlier study (Tomlinson &

Johnston, in preparation). However, the liquid-reared group failed to dishabituate, evidence that they failed to process the spatial relationship of the odor cues.

Two interesting sets of questions arise from this pilot work. First, why do the liquid-reared animals not dishabituate after a change in the spatial location of the odor cues? There are several possible reasons for their failure to dishabituate on the task. The liquid-rearing experience may have disrupted sensory or perceptual processes required by the task demands; however, this seems unlikely since all animals exhibited normal habituation to the arrangement of odor cues in session 2. There are at least three other possibilities which cannot be resolved on the basis of the pilot study. First, since the task forced hamsters to adopt an allocentric frame of reference during session 3, the failure to detect the spatial change may have resulted from an inability to integrate the odor cues into a configural relationship. Second, the animals may have been unable to process even simple associations related to spatial information. If so, we would expect them to be unable to detect a spatial change using an egocentric strategy. Finally, the animals may have been unable to integrate the olfactory cues and the visual component (striped pattern) of the test space. This last possibility would be considered an intersensory problem.

A second set of questions raised by the pilot study concerns the developmental mechanism by which liquid rearing affects spatial processing development. There is no reason to assume that the liquid food was directly responsible for the deficit, as it provided the same

nutrition as the solid food. There did not appear to be any gross anatomical or morphological differences between the liquid-reared and normally reared groups; furthermore, there were no differences in initial levels of exploration which one might expect if one group was suffering from severe malnutrition. However, the possibility remains that the liquid diet could have affected neurological areas necessary for successful spatial processing (Castro & Rudy, 1987). A further possibility was suggested by the informal observation that liquid-rearing curtailed early exploratory behavior of the pups. The liquid-reared pups left the nest quite frequently but their mothers returned them to the nest almost as soon as they had left. Thus, liquid food appears to affect maternal behavior, making the dam more protective, or at least more likely to direct attention towards the pups. This protective behavior, and the resulting restrictions on the pups' exploratory behavior, may have been a primary reason for the spatial processing deficits.

Summary

Open-field studies have provided demonstrations of spatial processing of visual (Thinus-Blanc & Ingle, 1985; Poucet, Chapuis, Durup, & Thinus-Blanc, 1987) and olfactory cues (Tomlinson & Johnston, in preparation). Although this work has enhanced our understanding of animal cognition, there has been little developmental research investigating spatial processing. Developmental studies have typically examined the abilities of the developing organism at different ages rather than looking at the "adult manifestations of early experience" (Cramer, Pfister, & Haig, 1987). In light of this, a primary objective

of this research was to determine the specific nature of the spatial processing differences between normally reared and liquid reared animals found in the pilot study and the developmental experiences responsible for those deficits.

The pilot task required hamsters to detect a change in the spatial location of two odor cues by adopting an allocentric rather than an egocentric frame of reference. Using an allocentric frame of reference to recognize the spatial change required the animal to remember the configurational properties of the test space. This study examines several hypotheses about the nature of the processing deficit seen in liquid reared hamsters. The deficit may have resulted from an inability to process configurational properties of the test space in the olfactory or visual modality. Alternatively, the animals may have been unable to process even simple associations related to spatial information in the olfactory or visual modality. A third hypothesis concerning the nature of the deficit is that liquid-reared animals were unable to integrate olfactory and visual components of the test space. There are also several hypotheses concerning the developmental mechanism for the processing problems seen in liquid-reared animals. The spatial processing problem could have occurred because liquid-reared pups experienced an overall decrease in the amount of exploratory experience during early development. A more interesting possibility is that a restriction of early exploratory experience occurred during a specific period of early development. A final hypothesis is that the liquid diet manipulation resulted in nutritional deficits known to attenuate configurational processing skills. This study consists of a series of

experiments which elucidate the nature of the processing deficit found in the LRG and identifies the rearing experience responsible for that deficit.

CHAPTER 2

Methods and Results

This study consisted of four experiments designed to investigate hypotheses concerning the nature of the spatial processing deficit found in the LRG discussed above; furthermore, the experiments evaluate hypotheses concerning the developmental mechanisms responsible for those processing deficits.

Methods and Materials

Subjects, colony maintenance, and breeding procedures

All animals used in these experiments were lab-reared Golden hamsters (Mesocricetus auratus). The hamsters were maintained in an indoor colony room in the Department of Psychology at UNC-Greensboro. Since hamsters are nocturnal creatures, the colony was on a reverse day/night cycle (14 hr light/10 hr dark), with lights off at 0530h. The animals were housed in polypropylene cages (22 x 43 x 21 cm) except as described below. All animals regardless of cage size were provided with commercial corncob bedding (Bed-D-Cob, Anderson Cob Division), an ample supply of shredded newspaper for nesting, and water ad libitum. Except as described below all animals were fed Purina Rodent Chow (#5001) supplemented by Purina Rabbit Chow and unsalted sunflower seeds. A colony of M. auratus has been maintained under these conditions for several years and the animals thrive and breed readily.

The breeding of hamsters for the present study was conducted as follows. Sometime during the first four hours of the dark cycle (0530h-0930h) a female was placed in the cage of a breeding male. Estrus

females quickly assumed a lordosis posture when placed in the male's cage, with copulation occurring almost immediately. If the female was not in estrus (i.e., if she failed to display lordosis) she was returned to her home cage and a second female was selected. Typically the pair separated after about 30 min and the female was returned to her home cage. On day 7 of gestation the female was transferred to a larger cage (40 x 55 x 20 cm) which served as home for her litter. Space limitations required this schedule which maximized the number of litters produced while allowing the dams ample time to settle into their surroundings. After being transferred to the larger cage, the dam was randomly assigned to a particular rearing condition (See Experiments 1 and 4 for details).

Females typically produced litters with between 10 and 12 pups. Litters were culled to 4 pups five days after parturition (P5) and weaned on P21. On P5 the culled animals were weighed and an average weight determined for each litter. After weaning pups were moved into individual plastic transport cages (floor area 700 cm²) with wire tops and water ad libitum. Testing occurred on the day of weaning and all pups were weighed again after testing. After testing pups were transferred to a large communal cage (floor area 2090 cm²) which contained other pups, a generous supply of rodent chow, and water ad libitum.

Experimental apparatus

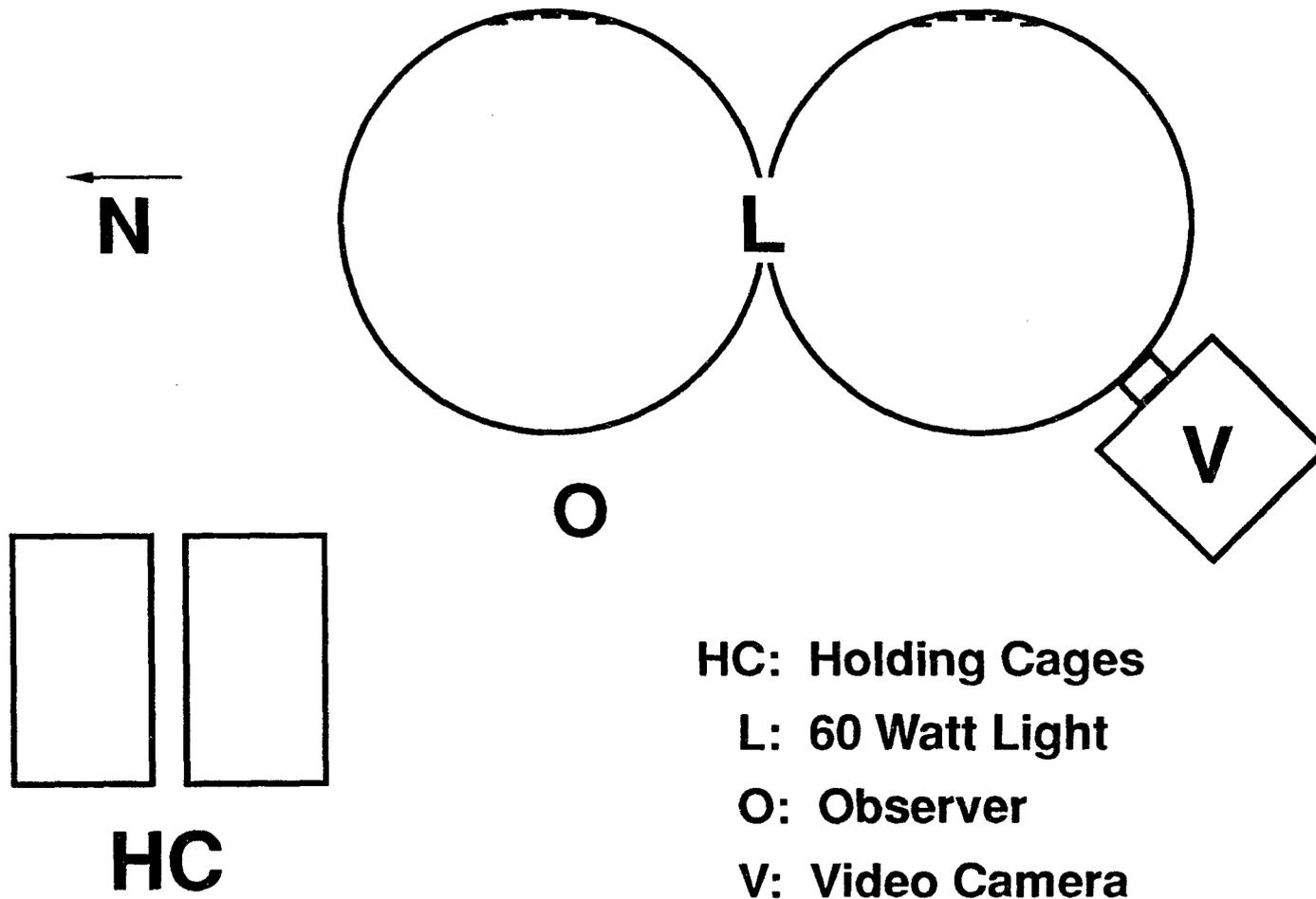
Testing was conducted in a circular plastic arena 91.5 cm in diameter with sides 42 cm high to prevent possible drafts from disturbing the experimental odor cues. The arena was located in a dark

testing room (9.0 x 6.9 m) with the temperature maintained between 21.7° and 24.4° C. The arena was illuminated by a 60W bulb suspended 114 cm above the floor. A white rectangle (21.5 x 37 cm) painted with equally spaced, 4-cm-wide black vertical stripes attached to the east wall of the arena, out of reach of the subjects, provided a conspicuous visual cue for orientation. The floor of the arena had a raised pattern that may have provided additional visual or tactile cues for orientation. Figure 1 shows the layout of the arena, camera, transport cages and the observer during scoring. Since odors and ultrasonic sounds from outside of the arena might have provided spatial cues during testing, the location of animal cages, the observer, and the camera remained invariant across all testing sessions and experiments.

Testing for spatial capabilities after weaning

All four pups in a litter were tested on the day of weaning (P21). Because hamsters are nocturnal, all testing was carried out in dim light during the first 4 hours of the dark cycle, a time when hamsters demonstrate high levels of activity (Landau, 1975). To increase the number of hamsters that could be tested during the early phase of the dark cycle and to provide a permanent record of behavior from a sample of the subjects, two subjects were tested simultaneously, the behavior of one of them being scored directly and that of the other videotaped for later scoring and data analysis. During each trial the observer recorded the number of times that the hamster's nose touched the object (a contact) and used a hand-held stopwatch to record the time that the hamster spent in contact with the objects. The videotapes allowed reliability of data collection to be determined.

FIGURE 1. Diagram of experimental apparatus



Reliability was determined in the following fashion. Twenty-one sessions were chosen in a pseudorandom fashion in order to determine reliability coefficients. Session selection was done such that each rearing condition in each experiment contributed a first, second and third session to the process. This was achieved by placing every animal number for a given condition by experiment in a box and randomly drawing a hamster number for rescoring session 1, session 2, and session 3. The numbers were drawn without replacement so that an animal could contribute only one session to the correlation process. Hamsters selected for the process are listed by experiment with variable values for both scorings in Table 1.

Each subject underwent one day of testing, involving a 15-min familiarization trial in the empty test arena, followed by three 10-min experimental sessions (S1 - S3). The subject was returned to its home cage for 10 min between successive sessions. Prior to S1 two objects were placed 25 cm apart along the north-south axis of the arena (Object characteristics described below). The subject was placed in the arena at the west wall at the beginning of S1 and S2 and allowed to explore for 10 minutes during each session. Before S3 the location of the two objects was switched; at the beginning of S3 the hamster was placed on the opposite side of the arena at the east wall (Experiments 1, 3 and 4) or at the west wall (Experiment 2). A small fan was used to protect against excessive buildup of the odors between sessions.

Table 1

Reliability of Scoring Method

Contact and contact times for animals used to assess reliability of scoring. Both sets of scores were gathered from analyses of video tapes.

<u>Litter</u>	<u>Hamster</u>	<u>Session</u>	<u>First Scoring</u>		<u>Second Scoring</u>	
			<u>Contacts</u>	<u>Time</u>	<u>Contacts</u>	<u>Time</u>
NRG8812	8954	1	28	11.31	29	10.58
NRG8815	8901	2	13	3.87	13	4.89
NRG8817	8910	3	17	4.85	17	5.93
LRG8902	8922	1	37	8.61	39	9.89
LRG8901	8918	2	8	2.11	8	2.86
LRG8901	8919	3	1	0.42	1	0.48
NRG8908	8950	1	43	14.65	41	13.21
NRG8910	8958	2	18	4.67	17	5.37
NRG8913	8968	3	20	6.43	20	6.20
LRG8903	8926	1	26	6.62	25	5.87
LRG8905	8936	2	11	3.81	11	4.08
LRG8909	8953	3	9	2.88	9	3.11
NRG8914	8972	1	14	5.32	14	5.56
NRG8915	8977	2	0	0	0	0
NRG8921	8994	3	44	13.89	40	11.97
LRG8912	8964	1	26	8.12	26	9.25
LRG8917	8982	2	11	7.33	11	8.12
LRG8916	8979	3	13	4.46	13	4.89
RRG8919	8987	1	18	4.36	17	4.01
RRG8924	89105	2	14	3.79	14	4.16
RRG8924	89107	3	7	1.97	7	2.00

Contacts: $r=0.988$

Time: $r=0.980$

Data Analysis

Habituation score

A measure of habituation was created for each hamster by subtracting their Session 2 scores (contact number and contact time) from their Session 1 scores. This process resulted in a contact habituation score and a contact time habituation score. Positive habituation scores reflect successful habituation. These habituation scores were compared using an ANOVA to determine if the experimental groups differed in their ability to habituate to the spatial layout. An additional ANOVA compared S1 levels of exploratory behavior (contacts and contact times) for the two experimental groups in each experiment.

Dishabituation score

A measure of dishabituation was calculated by subtracting Session 2 scores from Session 3 scores for each hamster. As with habituation scores, this resulted in a contact dishabituation score and a contact time dishabituation score. Positive dishabituation scores reflect successful dishabituation while negative or zero scores reflect continued habituation. These dishabituation scores were compared using an ANOVA to determine if the experimental groups differed in their ability to dishabituate following a change in the spatial layout of the arena. An additional ANOVA compared S3 levels of exploratory behavior (contacts and contact times) for the two experimental groups in each experiment to determine if there were differences in the exploratory behavior after a change in the spatial location of the two objects.

Experiment 1

Tomlinson and Johnston (in preparation) demonstrated that hamsters can employ an allocentric strategy to detect changes in the spatial locations of olfactory cues. Those findings indicate that hamsters remember configurational information derived from the odor cues in a familiar space even when the odor cues are of no biological significance (they were not pheromones). The results of the pilot study suggested that pups reared on a liquid diet could not remember the configurational layout of olfactory cues, perhaps because the diet caused the dams to restrict their pups' early forays from the nest. In Experiment 1 pups reared on either a liquid diet (LRG) or a normal (solid) diet (NRG) were tested for their ability to remember the spatial locations of two odor cues. Furthermore, Experiment 1 examined the early exploratory experiences of animals in both groups to see if the LRG exhibited lower levels of early exploratory behavior.

Methods and Materials

Subjects

Four females were assigned to a normal-rearing group (NRG) and four females assigned to a liquid diet which was intended to induce protective mothering styles (LRG). Thus, four litters made up each group. The NRG was fed as described above. Females in the LRG received a bottle of Kitten Milk Replacement (Borden) each morning starting on day seven of gestation.

Experimental apparatus

Two identical objects (visual cues) and two distinct odors (olfactory cues) were used in Experiment 1. The objects were glass

cheese shakers (CS) with a stainless steel top (8.8 cm in height and 5.3 cm in diameter). Each object was filled with sand for stability and had a square of gauze secured under its perforated cap for application of the odorant. Two floral potpourri oils (Carolina Fragrance Trading Company, Charlotte, NC), honeysuckle (H) and gardenia (G), were used as odorants.

Procedures

Measurement of exploratory behavior before weaning.

Daily observations were made on a sample of litters in each group in an effort to confirm that dams in the LRG did indeed restrict the activity of their pups more than did dams in the NRG. Observations made during the pilot study suggested that there might be differences in the overall amount of exploration for the LRG and the NRG; therefore, variables associated with early exploratory forays were quantified. Data collection proceeded as follows. Litters were videotaped using a time-lapse mechanism which took a 1-sec picture of the home cage every 60 secs. Camera and time limitations made it impossible to tape every litter on every day of development, but several litters from each group were taped on each day between P7 and P20. By placing the camera directly above the cage a sample of the litter's exploratory behavior was taken once every minute. The timer automatically shut the camera off after 10 hrs of recording. Recording began at 1000h each day, allowing 5.5 hrs of dark and 4.5 hrs of light sampling. For this study it was not important which time interval was being sampled, but it was important to make sure that all samples were taken from the same period of time. In this case 1000 hrs was used as a starting time because that

allowed the camera to be used in data collection for the processing experiments. The end result of the time-lapse recordings was that 600 frames of the litter's behavior for each day recorded (P7-P20) were obtained. For every fifth frame the number of pups out of the nest (frequency of exploration for the litter) and their distance from the nest (degree of exploration for the litter) was scored from the videotape. For purposes of this study the nest was defined as the circle of shredded paper within which the dam feeds the pups.

The purpose of collecting these data was to help elucidate the differences in the early exploratory experiences of the two groups. This was achieved in two ways. First, daily measures of exploratory activity were made for each rearing condition. Camera and time limitations prevented collecting enough samples for a statistical comparison of group changes across time, but the mean (n=4 litters/group) number of animals out of the nest and their cumulative distance from the nest are plotted in Figures 2a and 2b for comparison. These figures provide evidence that the LRG had fewer and less extensive forays from the nest than did the NRG. Secondly, although a statistical comparison of changes across time was not possible, an ANOVA was conducted on measures of exploratory activity for P14. P14 was chosen because Schoenfeld and Leonard (1982) indicate that a surge in sniffing behavior reaches its peak by that day. Furthermore, Johnston and Coplin (1979) demonstrated that an increase in exploratory behavior occurs on P14. Processing olfactory cues while exploring may be an important developmental experience for subsequent spatial processing and since P14

FIGURE 2a

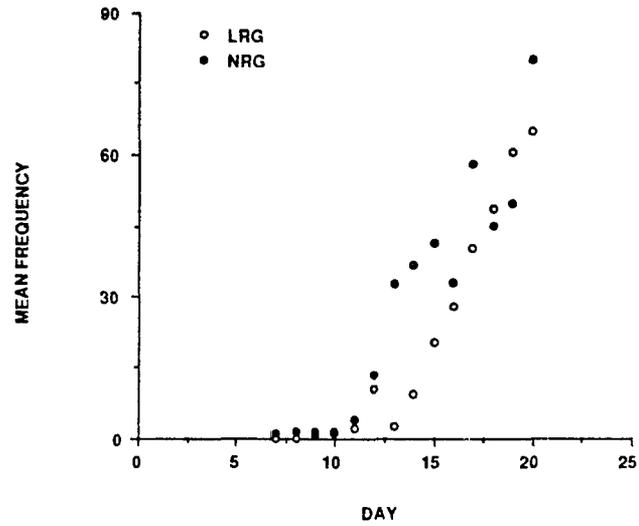


FIGURE 2b

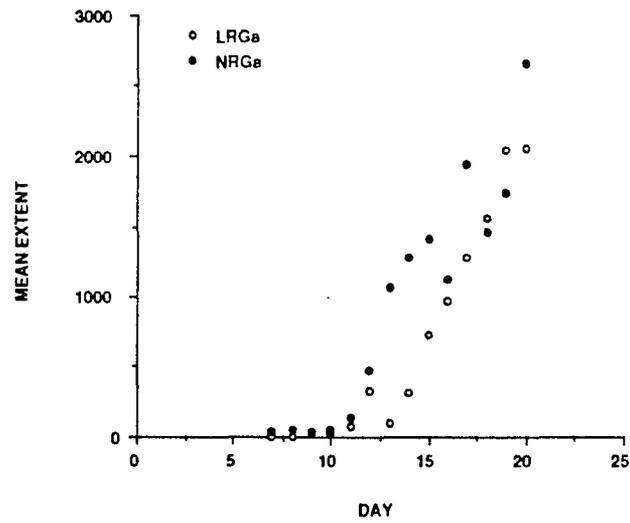


Figure 2. Mean cumulative number (2a) and mean cumulative distance (2b) of pups out of nest for NRG and LRG on each day of development P7 to P20.

provides a time when sniffing and exploration peaks, it seems that exploratory activity on that day may differ for the two groups.

Testing for spatial capabilities after weaning

Prior to S1 the two cheese shakers, one scented with gardenia oil (G), the other with honeysuckle oil (H), were placed 25 cm apart along the north-south axis of the arena. The north-south placement of the odorants was G-H for half of the litters in each group and H-G for the other half. The subject was placed in the arena at the west wall at the beginning of S1 and S2 and allowed to explore for 10 minutes during each session. Before S3 the location of the two cheese shakers and their associated olfactory cues was switched; at the beginning of S3 the hamster was placed on the opposite side of the arena at the east wall. As in the pilot study, this procedure required the animal to use an allocentric strategy for detecting the change in the location of the odors and thus tested its ability to process configurational spatial information.

Results

(1) Comparisons of early exploratory experience

Figure 2a illustrates the average cumulative frequency of pups in each group that were out of the nest for each day of development. Figure 2b illustrates the average cumulative distance from the nest of pups in each group that were out of the nest on each day of development. Comparison of mean cumulative scores for P14 indicated that the NRG had more pups out of the nest than did the LRG (36.67 vs 9.25) [$F(1,5) = 6.87, p = 0.047$] and had a larger mean cumulative distance from the nest (1282.67 vs 313.00) [$F(1,5) = 7.38, p = 0.042$].

(2) Comparison of pups' weights

There were no differences in the animals' mean weights on either P5 (6.40 vs 6.70) [$F(1,6) = 0.42, p = 0.541$] or P21 (32.60 vs 28.88) [$F(1,6) = 3.75, p = 0.101$].

(3) Reliability of scoring procedures.

An analysis of the reliability of scoring procedures yielded coefficients of 0.988 for contacts and 0.980 for contact time (Table 1).

(4) Initial exploration and habituation

Analyses conducted on mean S1 contacts revealed no statistically significant differences between the NRG and the LRG (28.56 vs 24.00) [$F(1,6) = 1.33, p = 0.292$]. Likewise, there were no differences in mean S1 contact times (10.62 vs 8.46) [$F(1,6) = 1.33, p = 0.293$]. Every animal, and thus both groups, exhibited fewer contacts and less contact time in S2 than in S1 showing that they all habituated to the presence of the two objects in the arena (Figure 3a & 3b). Furthermore, a measure of habituation derived by subtracting S2 scores from S1 scores revealed no differences in mean number of contacts (16.50 vs 12.81) [$F(1,6) = 1.58, p = 0.256$] or mean contact time habituation (6.59 vs 4.64) [$F(1,6) = 1.99, p = 0.0208$] between the two groups.

(5) Dishabituation during session 3

Between S2 and S3, both the number of contacts and the contact time dishabituated in the NRG, but neither measure dishabituated in the LRG (Figures 3a & 3b). An ANOVA revealed a statistically significant effect of experimental group (rearing condition) on mean number of contacts in S3 [$F(1, 6) = 8.50, p = 0.0271$], the NRG having more contacts than the LRG (18.31 vs 9.62). The NRG also had more time in contact

FIGURE 3a

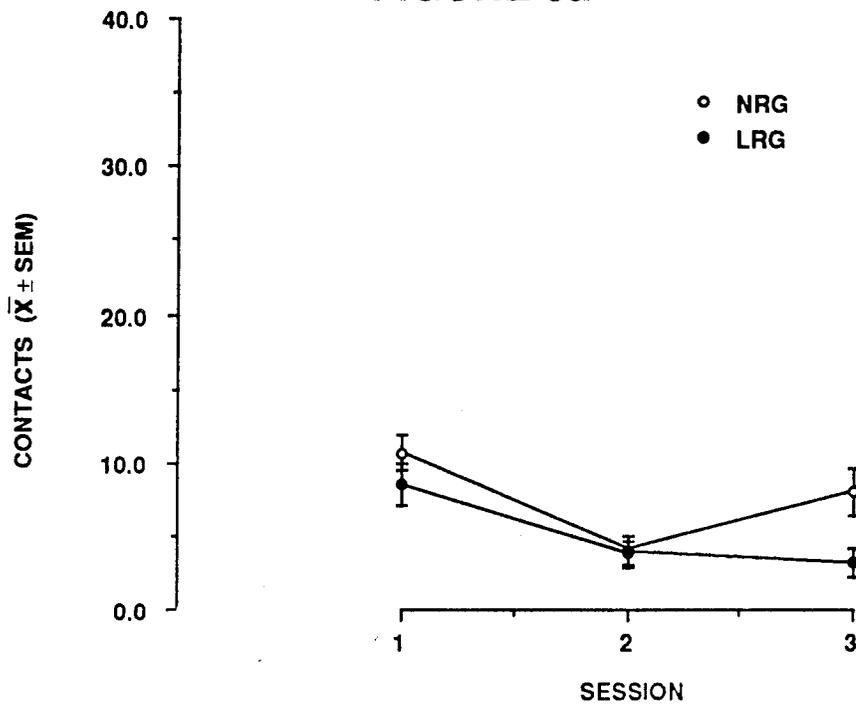


FIGURE 3b

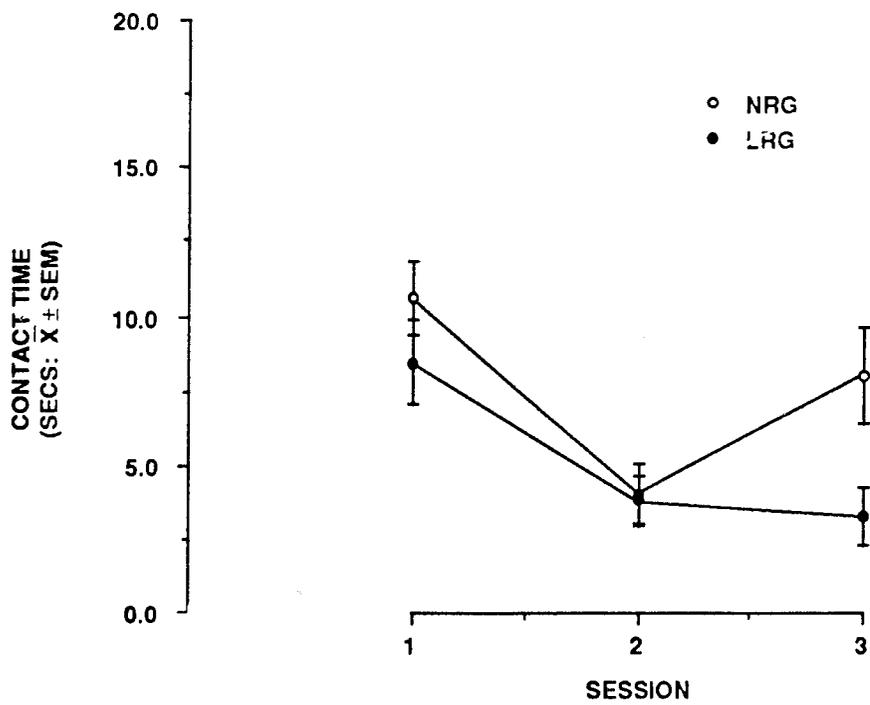


Figure 3. Mean number contacts (3a) and mean contact times (3b) by session and group for Experiment 1 ($\bar{X} \pm SEM$).

with the objects during S3 than did the LRG (8.03 vs 3.26) [$F(1,6) = 6.51, p = 0.044$]. The dishabituation scores for contact number and contact time (obtained by subtracting S2 scores from S3 scores) are shown in Figures 4a and 4b. Animals in the NRG had positive dishabituation scores on both measures, whereas the LRG's dishabituation scores were negative. ANOVAs performed on both contact-number and contact-time dishabituation scores revealed statistically significant differences between groups in both cases [mean contact number (6.25 vs -1.56): $F(1,6) = 8.57, p = 0.026$; mean contact time (4.00 vs -0.56): $F(1,6) = 18.54, p = 0.0051$].

Discussion

As expected, pups raised on liquid diets failed to demonstrate configurational memory for olfactory cues as indicated by their failure to dishabituate in the presence of a new spatial arrangement of olfactory cues when required to use an allocentric strategy of responding. These results confirm the findings of the pilot study, namely that liquid-reared hamsters do not process the configurational relationship of olfactory cues. Two interesting questions arise from this experiment. First, why do the pups fail to develop the ability to detect the spatial change from an allocentric frame of reference? Identifying the developmental precursor of this processing deficit may shed light on conditions necessary for typical development of such skills. The observations made on the litters indicate that levels of exploration (frequency and extent) were lower for the LRG than for the NRG, supporting informal observations made during the pilot study. These observations suggest that at least one difference between the two

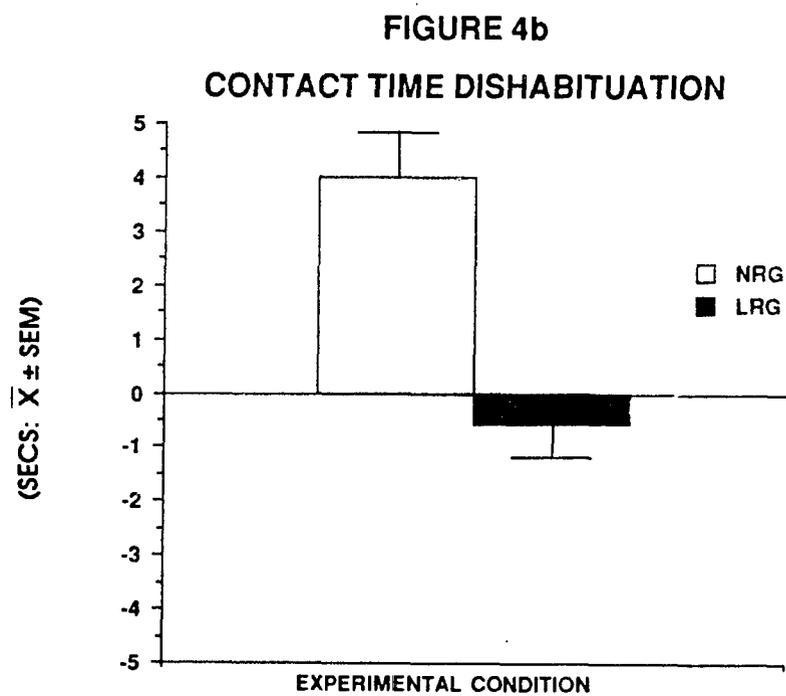
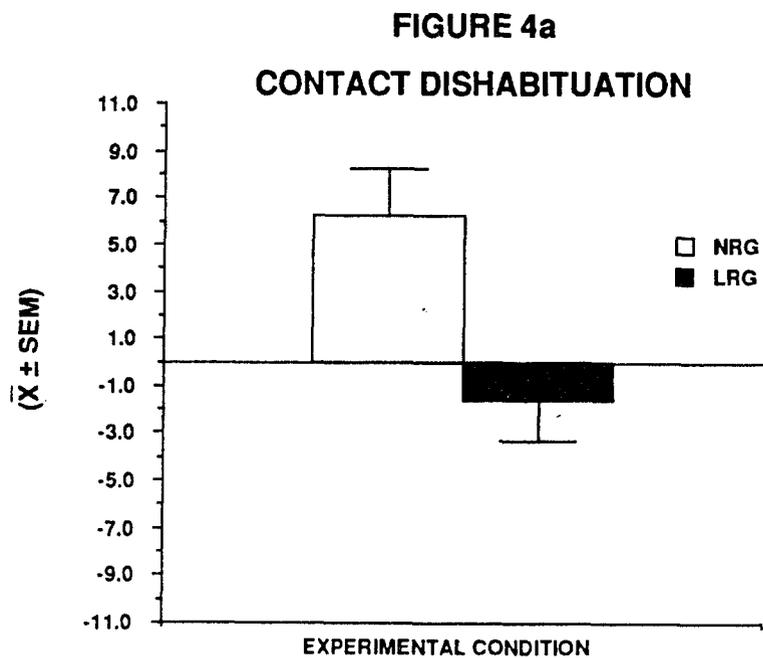


Figure 4. Mean contact dishabituation scores (4a) and mean contact time dishabituation scores (4b) for NRG and LRG in Experiment 1 ($\bar{X} \pm \text{SEM}$).

groups was the amount of exploratory experience allowed the pups. Although there were no weight differences between the groups, a subtle nutritional deficit may have contributed to the inability to process the configurational arrangement of olfactory cues. This question was addressed directly in Experiment 4, in which the early exploratory experience of pups raised on a normal (solid) diet was restricted.

The second question raised by this experiment concerns the actual nature of the spatial deficit exhibited by pups in the LRG. There are several possible reasons why the LRG failed the task, including: (1) a specific inability to process the configurational properties of the odor cues; (2) a more general inability to process even simple spatial associations; (3) an even more general inability to process olfactory cues of any kind; or (4) an inability to integrate the olfactory and visual components of the test space. It seems unlikely that the animals were unable to process olfactory cues at all since they did habituate to the odors in the arena. Experiment 2 examined the first two of the other three possibilities by comparing the performance of liquid-reared and normally reared pups on a less demanding spatial task.

Experiment 2

Whereas Experiment 1 required pups to use an allocentric strategy, and hence process the configurational properties of spatial cues, Experiment 2 assessed the performance of a NRG and a LRG on a simple spatial task in which the animals could adopt an egocentric frame of reference and use simple associations formed in S1 and S2 to detect the spatial change in S3. If the rearing experience of the LRG attenuates general spatial processing then they should fail to dishabituate during

S3. However, if liquid rearing specifically affects configurational memory systems then their performance should not differ from animals in the NRG.

Methods and Materials

Subjects

Rearing conditions and group assignment were the same as in Experiment 1.

Procedures

The procedures for Experiment 2 were the same as for Experiment 1 with one exception. On the critical experimental trial, S3, the animals entered the arena from the West side. This procedural difference means that animals entered the arena from the same side on all three trials, and could therefore use an egocentric frame of reference to process the spatial cues. The egocentric perspective does not require configurational memory to detect the change in the spatial location of the odor cues. Thus, unlike Experiment 1, Experiment 2 allowed hamsters to use simple associations formed in S1 and S2 to detect the spatial change in S3.

Results

(1) Initial exploration and habituation

As in Experiment 1 there were no statistically significant differences for mean S1 contacts (29.15 vs 26.00) [$F(1,6) = 0.77, p = 0.414$] or mean contact times (10.94 vs 9.99) [$F(1,6) = 0.19, p = 0.680$] between the NRG and the LRG. Every animal, and thus both groups, exhibited fewer contacts and less contact time in S2 than in S1 showing that they all habituated to the presence of the two objects in the arena

(Figures 5a & 5b). Mean habituation scores revealed no differences in habituation between the two groups for contacts (17.45 vs 14.44) [$F(1,6) = 0.64$, $p = 0.454$] or contact time (6.64 vs 6.56) [$F(1,6) = 0.00$, $p = 0.974$].

(2) Dishabituation during Session 3

Between S2 and S3, the number of contacts and the contact time dishabituated for both groups (Figures 5a & 5b). An ANOVA found no statistically significant differences between experimental groups on mean number of contacts in S3 (13.10 vs 15.12), [$F(1, 6) = 0.32$, $p = 0.593$] or for mean time in contact with the objects during S3 (4.60 vs 5.16) [$F(1,6) = 0.26$, $p = 0.629$]. The mean dishabituation scores for contact number and contact time are shown in Figures 6a and 6b. Animals in both groups had positive dishabituation scores on both measures. ANOVAs performed on both contact-number and contact-time dishabituation scores revealed no statistically significant differences between groups for either variable [mean contact number (1.40 vs 3.56): $F(1,6) = 0.38$, $p = 0.560$; mean contact time (0.31 vs 1.73): $F(1,6) = 1.62$, $p = 0.250$].

Discussion

Experiment 2 clearly demonstrated that when allowed to adopt an egocentric frame of reference, and thus use simple associative memories, all pups, regardless of rearing condition, were able to detect a change in the spatial location of odor cues. These results suggest that the LRG's failure to detect a change in Experiment 1 resulted from an attenuated ability to form configural associations. The animals may not have processed any configurational information or they may have formed partial configural associations, either of which would suggest a problem

FIGURE 5a

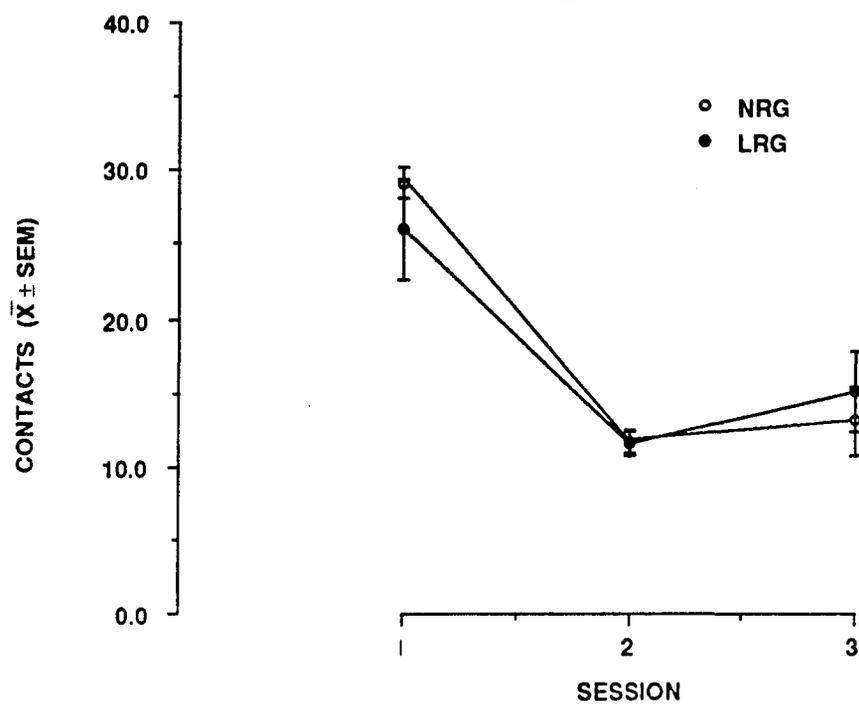


FIGURE 5b

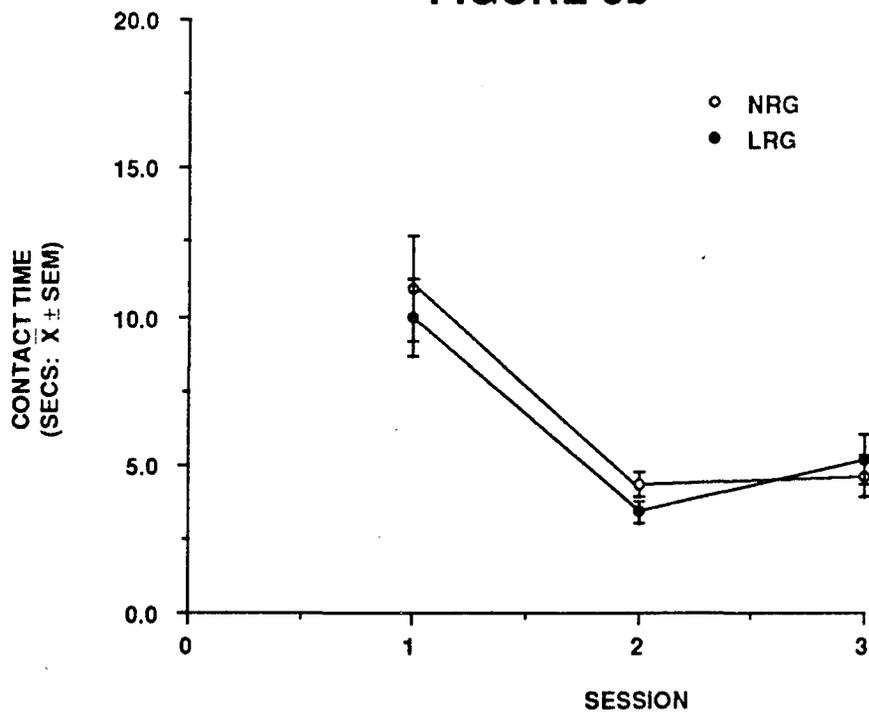


Figure 5. Mean number contacts (5a) and mean contact times (5b) by session and group for Experiment 2 ($\bar{X} \pm SEM$).

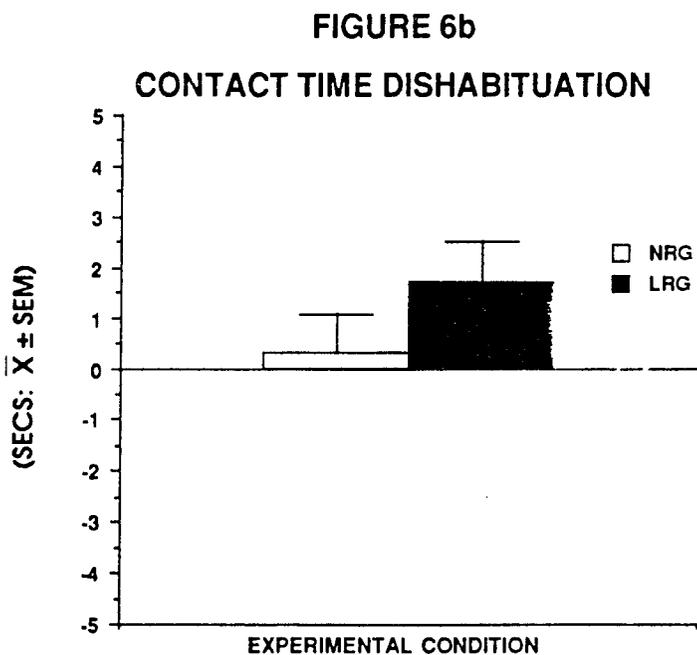
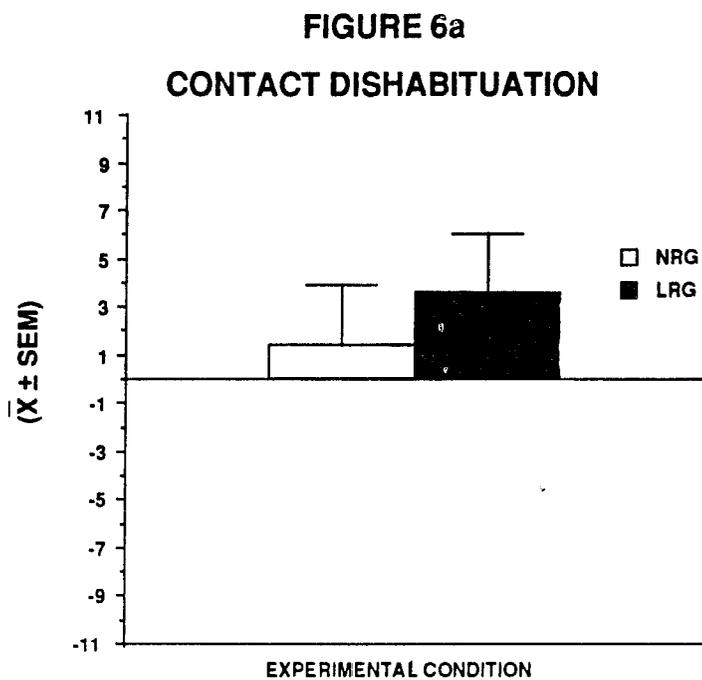


Figure 6. Mean contact dishabituation scores (6a) and mean contact time dishabituation scores (6b) for NRG and LRG in Experiment 2 ($\bar{X} \pm \text{SEM}$).

with processing configural associations. However, the results do not demonstrate whether the processing deficit in the LRG pups was a general spatial deficit or was specific to the olfactory modality. The restricted experience of the LRG on P14 occurred during a period when olfactory cues mediate the pups' behavior (see discussion above) and so the inability to form configurational associations may be specific to the olfactory modality. On the other hand, the experience may have resulted in a general inability to form configurations regardless of the modality.

Experiment 3

Experiment 3 assessed the generality of the deficit by testing a NRG and a LRG for their ability to detect a change in the spatial location of visual cues when adopting an allocentric frame of reference. If the rearing experience is specific to the olfactory modality then all animals should dishabituate in the presence of the new spatial arrangement of visual cues.

Methods and Materials

Subjects

Subjects and group assignment were the same as in Experiment 1.

Experimental apparatus

The experimental apparatus and testing room were the same as in Experiment 1 with the following exceptions. First no odor cues were used in this experiment. Instead, two distinct visual cues were used, a glass chutney jar (11.5 cm in height and 6.0 cm in diameter) with a metal top and a large glass cheese shaker (LCS) with a stainless steel top (14.5 cm in height and 7.5 cm in diameter). Again each object was

filled with sand for stability. Other aspects of the testing apparatus were identical to those used in Experiment 1.

Procedures

The procedures for Experiment 3 were the same as for Experiment 1.

Results

(1) Initial exploration and habituation

As in Experiments 1 and 2 there were no statistically significant differences for mean S1 contacts (30.15 vs 25.44) [$F(1,6) = 0.26, p = 0.627$] or mean contact times (13.65 vs 12.69) [$F(1,6) = 0.08, p = 0.783$] between the NRG and the LRG. Again every animal, and thus both groups, exhibited fewer contacts and less contact time in S2 than in S1 showing that they all habituated to the presence of the two objects in the arena (Figures 7a & 7b). Mean habituation scores revealed no differences in habituation between the two groups for contacts (17.88 vs 15.29) [$F(1,6) = 0.79, p = 0.410$] or contact time (8.43 vs 7.78) [$F(1,6) = 0.21, p = 0.660$].

(2) Dishabituation during Session 3

Unlike Experiment 1 the number of contacts and the contact time dishabituated during S3 for both groups (Figures 7a & 7b). An ANOVA found no statistically significant differences between experimental groups on mean number of contacts in S3 (19.77 vs 13.91), [$F(1, 6) = 0.59, p = 0.471$] or for mean time in contact with the objects during S3 (8.22 vs 6.40) [$F(1,6) = 0.36, p = 0.568$]. The mean dishabituation scores for contact number and contact time (obtained by subtracting S2 scores from S3 scores) are shown in Figures 8a and 8b. Animals in both groups had positive dishabituation scores on both measures. ANOVAs

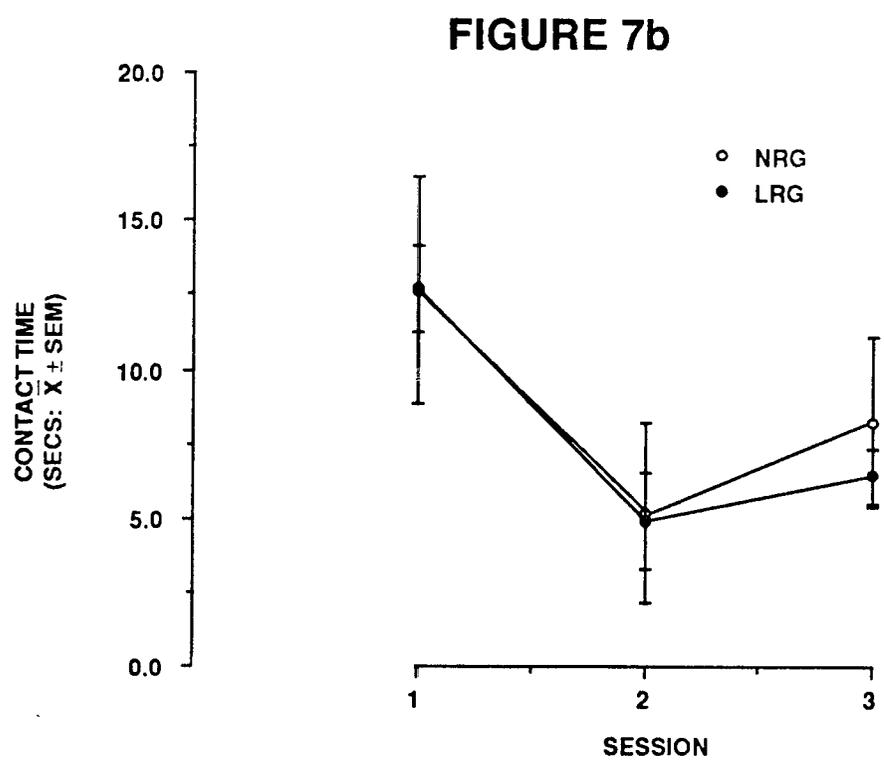
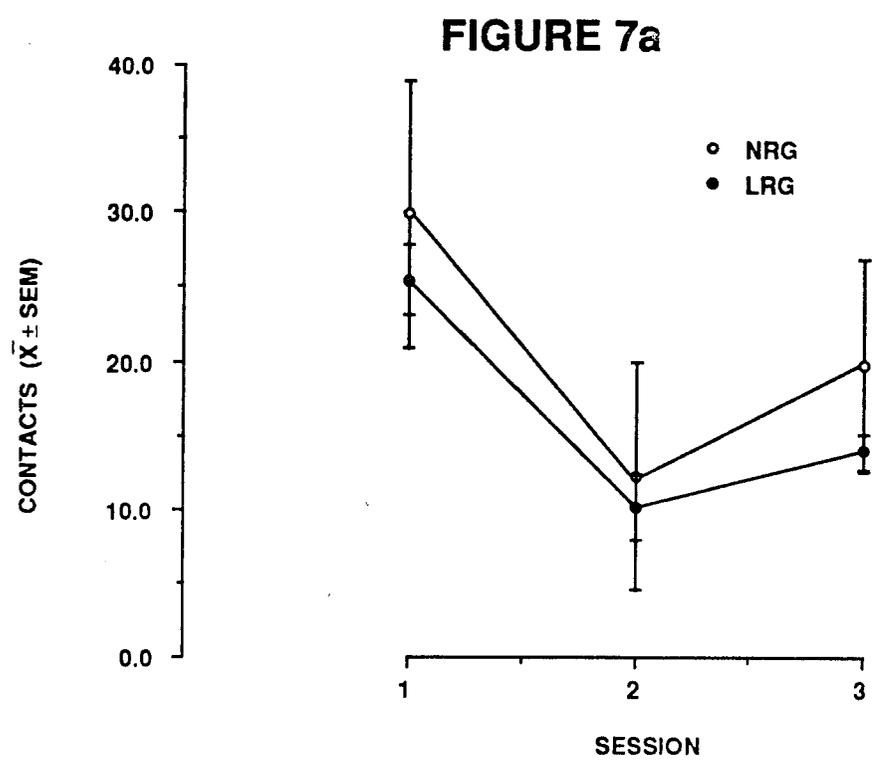


Figure 7. Mean number contacts (7a) and mean contact times (7b) by session and group for Experiment 3 ($\bar{X} \pm SEM$).

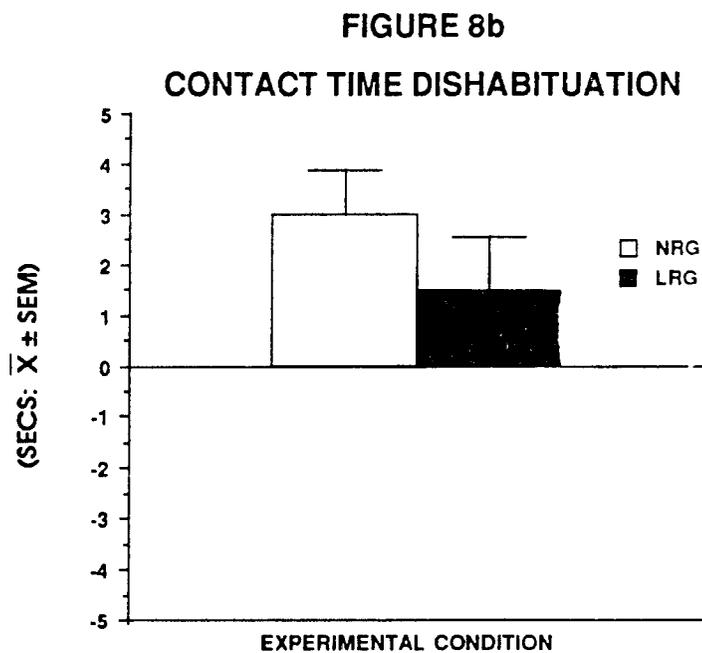
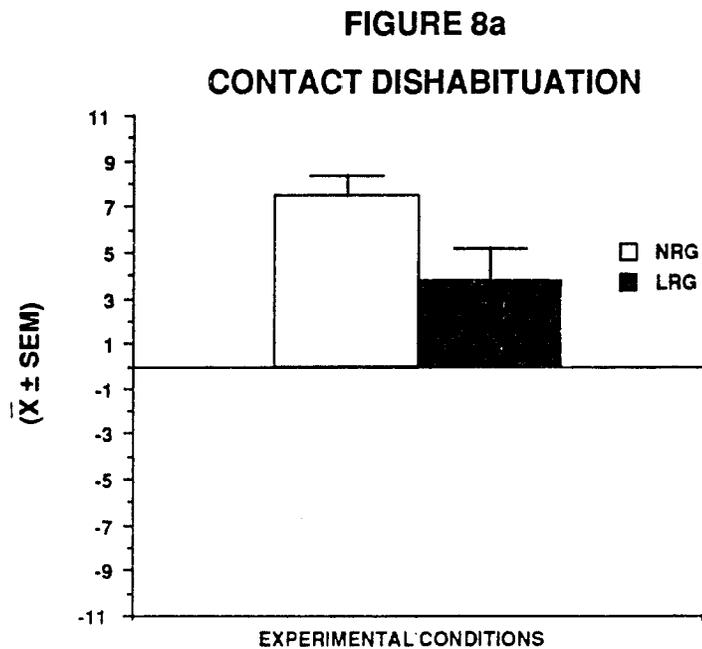


Figure 8. Mean contact dishabituation scores (8a) and mean contact time dishabituation scores (8b) for NRG and LRG in Experiment 3 ($\bar{X} \pm \text{SEM}$).

performed on both contact-number and contact-time dishabituation scores revealed no statistically significant differences between groups for either variable [mean contact number (7.50 vs 3.77): $F(1,6) = 4.93$, $p = 0.068$; mean contact time (3.00 vs 1.49): $F(1,6) = 1.16$, $p = 0.3221$].

Discussion

The results of Experiment 3 indicated that hamsters in the LRG can process configurational information derived from visual cues as well as hamsters in the NRG. Thus, their inability to detect a spatial change in the odor cues in Experiment 1 occurred not because of an inability to process configurational information generally but because of an inability to process the configurational properties of olfactory cues. These findings are important for at least two reasons. First, they suggest that certain early experiences can disrupt cognitive functioning mediated by one modality without having an impact on processing in a second modality. Furthermore, these results indicate that the liquid diet used to lower the early exploratory behavior of the pups did not result in malnourished animals. Malnourished animals typically experience retarded development of the hippocampus (Patel, 1983; Jordan & Clark, 1983), a brain area which has been shown to underlie configurational memory for visual cues (Sutherland & Rudy, 1989). If the liquid-reared animals in the present study had been malnourished they would have failed to dishabituate during S3 of this experiment because of inadequate hippocampal development.

However, the possibility does exist that animals in the LRG did experience some subtle nutrient deficiency that only affected the processing of configurational information in the olfactory modality and

so was responsible for the attenuated behavioral performance in Experiment 1. Experiment 4 was conducted to strengthen the argument that it was the restriction of exploratory behavior between P8 and P14 of development that led to the subsequent inability to process olfactory configurations by testing a restricted-rearing group (RRG) under Experiment 1 procedures.

Experiment 4

The hypothesis that the deficit observed in Experiment 1 was the result of subtle malnutrition rather than of restricted early exploration can be tested directly by rearing hamsters on a normal (solid) diet but restricting their early exploratory forays from the nest. This test was conducted in Experiment 4.

Methods and Materials

Subjects

Four pregnant females, designated a Restricted-Rearing Group (RRG), were placed in the same large breeding cages used in earlier experiments. However, each cage contained a second, smaller cage (16 x 28 x 13 cm) in one corner. Newspaper strips were placed in this second cage to encourage its use as a nest area. All four females used the smaller cage as a nest area. The height of the smaller cage's walls prevented pups from exploring the larger cage until after P13. All pups in this group were able to climb out of the smaller cage by the afternoon of P14 and no pups were observed out of this cage before the afternoon of P13. Thus, the cage restricted the exploratory experiences of the pups during the period when olfaction mediates behavior (P8-P14).

The behavior of the mothers did not appear to be affected by the presence of the smaller cage.

Separate NRG and LRG were not reared separately for this experiment. Instead, data from the NRG and LRG in Experiment 1 were used for purposes of comparison.

Procedures

Procedures were identical to those used in Experiment 1.

Results

(1) Initial exploration and habituation

One litter in the RRG failed to habituate and generally displayed low levels of exploratory behavior. This litter was dropped from all analyses; therefore, Experiment 4 analyses were conducted with three RRG litters and four litters each in the LRG and NRG.

There were no statistically significant differences between groups (NRG vs LRG vs RRG) for mean number of S1 contacts (28.56 vs 24.00 vs 25.25) [$F(2,8) = 0.62, p = 0.563$]. Likewise, mean contact times (10.62 vs 8.46 vs 6.78) did not differ statistically for the two groups [$F(2,8) = 2.07, p = 0.189$]. Although one RRG litter failed to habituate, three groups exhibited fewer contacts and less contact time in S2 than in S1 showing that they habituated to the presence of the two objects in the arena (Figures 9a & 9b). Mean habituation scores revealed no differences in contact habituation scores (16.50 vs 12.81 vs 12.67) [$F(2,8) = 1.30, p = 0.325$] or in contact time habituation scores (6.59 vs 4.64 vs 3.56) [$F(2,8) = 2.76, p = 0.122$].

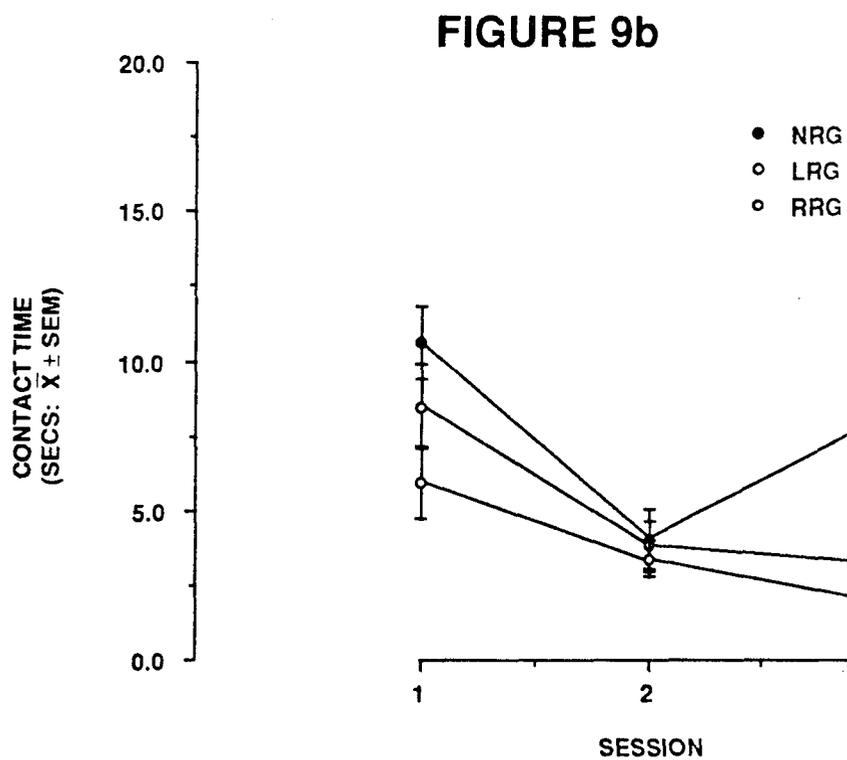
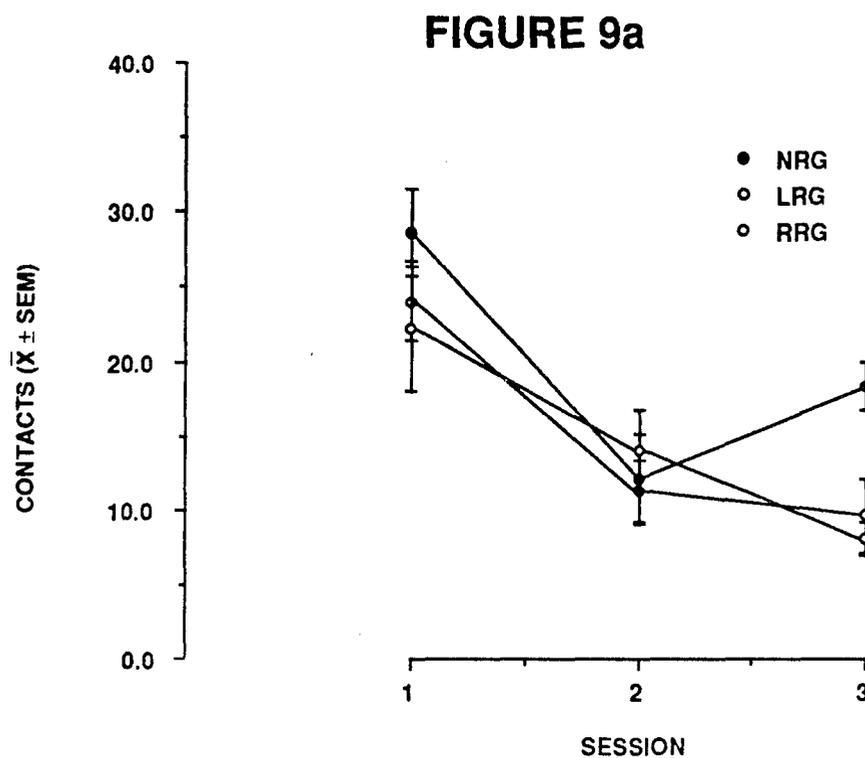


Figure 9. Mean number contacts (9a) and mean contact times (9b) by session and group for Experiment 4 ($\bar{X} \pm \text{SEM}$).

(2) Dishabituation during Session 3

Between S2 and S3, both the number of contacts and the contact time dishabituated in the NRG, but neither measure dishabituated in the RRG or LRG (Figures 9a & 9b). An ANOVA revealed a statistically significant effect of experimental group on mean number of contacts in S3 (18.31 vs 9.62 vs 7.58) [$F(2,8) = 8.10, p = 0.0121$]. Furthermore, an orthogonal comparison of the groups revealed that the NRG on average had more contacts than the LRG or RRG [$F(1,8) = 16.09, p = 0.0041$]. An additional orthogonal comparison indicated that the LRG and the RRG did not differ statistically [$F(1,6) = 0.48, p = 0.5071$]. There was a significant group effect on mean S3 contact times (8.03 vs 3.25 vs 1.90) [$F(2,8) = 7.19, p = 0.0161$]. The NRG also on average had more time in contact with the objects during S3 than did the LRG or RRG [$F(1,8) = 14.18, p = 0.0061$]. However, as with S3 contacts there were no statistically significant differences between the LRG and the RRG [$F(1,6) = 0.60, p = 0.4611$].

The dishabituation scores for contact number and contact time are shown in Figures 10a and 10b. Animals in the NRG had positive dishabituation scores on both measures, whereas the LRG and RRG's dishabituation scores were negative. ANOVAs performed on both contact-number and contact-time dishabituation scores revealed statistically significant differences between groups in both cases [mean contact number (6.25 vs -1.56 vs -5.00): $F(2,8) = 8.61, p = 0.010$; mean contact time (4.00 vs -0.56 vs -1.32): $F(2,8) = 15.46, p = 0.0021$]. Once again orthogonal contrasts revealed that the group effect resulted from a difference between the NRG and the two other groups [mean contact

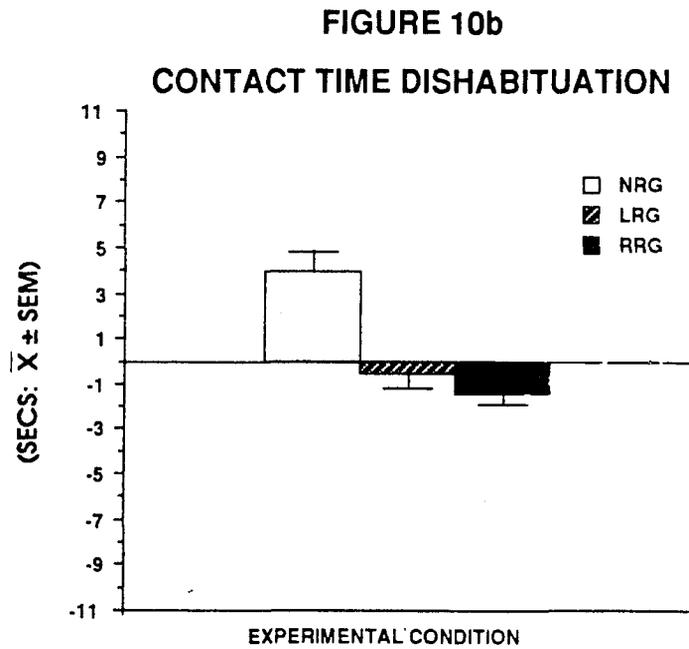
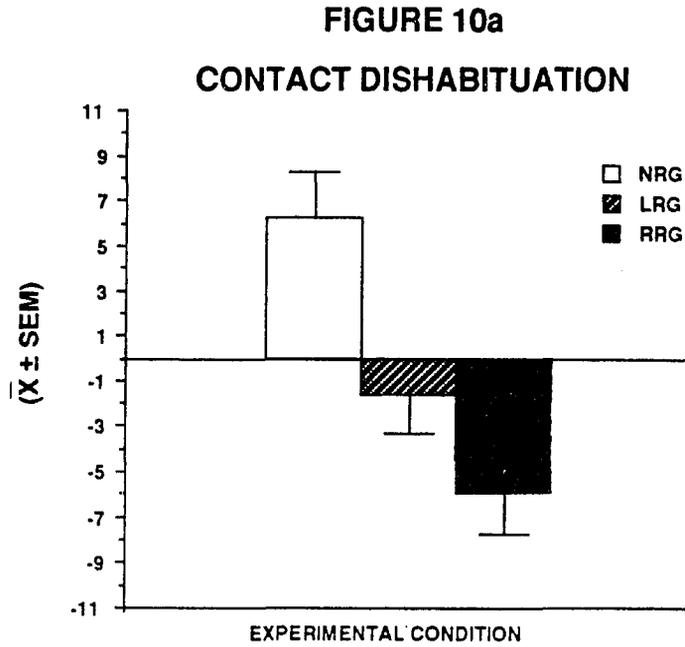


Figure 10. Mean contact dishabituation scores (10a) and mean contact time dishabituation scores (10b) for NRG and LRG in Experiment 4 ($\bar{X} \pm \text{SEM}$).

number: $F(1,8) = 16.48$, $p = 0.004$; mean contact time: $F(1,8) = 30.88$, $p = 0.0005$]. As with the other analyses there were no differences between the RRG and the LRG [mean contact number: $F(1,6) = 1.45$, $p = 0.262$; mean contact time: $F(1,6) = 0.49 = 0.503$].

Discussion

The results of Experiment 4 parallel those of Experiment 1 and demonstrate that restricting the exploratory experience of hamsters during the period when olfaction mediates behavior results in an inability to form configurational associations between odor cues. Thus the hypothesis that the effects of liquid rearing shown in the first three experiments were the result of subtle nutritional deficiencies can be rejected. Rather, the significant effect of liquid rearing was to restrict the pups' early exploratory behavior, producing the deficits in spatial information processing demonstrated in Experiments 1, 2, and 3.

CHAPTER 3

General Discussion

The primary objectives of this research were to determine the specific nature of the spatial processing differences found in animals reared on a liquid diet and to identify the developmental experiences responsible for those deficits. In Experiment 1 hamsters were raised on either a normal or a liquid diet. Animals reared on the liquid diet exhibited fewer and less extensive forays from the nest between P8 and P14 than did normally-reared pups. On the day of weaning the normally-reared and liquid-reared hamsters were allowed to habituate to the spatial arrangement of two odor cues. Following habituation the pups were returned to the test arena and allowed to explore a novel spatial arrangement of the familiar odor cues. The animals were forced to adopt an allocentric rather than an egocentric frame of reference because of a change in point of entry on the dishabituation trial. Liquid-reared but not normally reared animals failed to dishabituate in the presence of the spatial change.

In Experiment 2 pups were again compared for the effect of liquid rearing on subsequent spatial performance; however, in this test animals were allowed to enter the arena from the same starting point on all three trials, permitting the use of a simpler, egocentric strategy for detecting the spatial change. All animals, regardless of rearing condition, dishabituated in the presence of the new spatial

configuration. In Experiment 3 all animals dishabituated in the presence of a change in the spatial relationship of visual cues, even though they were again required to adopt an allocentric frame of reference. Experiment 4 demonstrated that hamsters reared on normal food, but experiencing a direct restriction of their early exploratory experience from P8 to P14, failed to dishabituate in the presence of a change in a familiar spatial relationship between odor cues when forced to adopt an allocentric frame of reference.

When taken together, the experiments in this study provide compelling evidence that exploratory experience during the period in development when olfaction begins to mediate behavior is necessary for species-typical development of configurational memory for olfactory cues in hamsters. The rearing effect did not extend to spatial processing generally since liquid-reared animals could detect a spatial change when allowed to adopt an egocentric frame of reference. Furthermore, the effect appeared to be quite specific to the olfactory modality; both groups demonstrated an ability to process the configurational properties of visual cues. The restricted-rearing group in Experiment 4 confirmed the hypothesis that restriction of exploratory experience between P8 and P14 was the developmental event responsible for the LRG's failure to dishabituate in Experiment 1. Thus, this study has answered important questions concerning both the experiences necessary for the normal development of spatial processing and the nature of the processing deficit that results from early restriction of exploratory behavior.

However, a number of interesting problems still remain. For example, hamsters may fail the allocentric spatial processing task

either (1) because they cannot integrate odor cues into a configuration or (2) because they cannot integrate the configuration of odor cues with the visually distinct striped pattern. The first alternative attributes the animals' behavior to an intramodal (olfactory) deficit in forming configurational associations (Sutherland & Rudy, 1989). The second attributes their behavior to an intermodal deficit involving integration of visual and olfactory cues. A simple test of these alternatives would involve rearing and testing hamsters under the same conditions as in Experiment 4 with two exceptions: First, the striped pattern in the arena would be replaced by a distinctive odor cue; second, the test sessions would be conducted in the dark, eliminating the possibility that the animals might use other visual cues for orientation. Under these conditions hamsters would be required to form configural associations among the odor cues alone, without interference from any visual cues. If the restricted experience in development disrupts intersensory functioning then all animals should dishabituate after a change in the layout of the odor cues. However, if the effect is on processing of olfactory configurations then the restricted group should fail to dishabituate on this task.

Another question concerns the point in spatial information processing at which impaired processing occurs. It may be that the restricted animals never detected the configural properties of the olfactory cues during the acquisition phase of processing (in Sessions 1 and 2), or that they never properly stored such associations (between Sessions 2 and 3). Alternatively, it could be that acquisition and storage processes are intact but that the animals cannot retrieve the

information during Session 3. The technique used in this study cannot distinguish among these alternatives and further research will be needed to identify which of these processes were disrupted by the restriction of early experience.

The observations made on litters in Experiment 1, together with the results of Experiment 4, indicate that liquid rearing reduces the amount of exploratory behavior during the period of development when olfaction begins to mediate the pups' behavior. In the liquid-reared groups of Experiments 1 - 3, the reduction appears to have resulted because dams restricted their pups' forays from the nest. This finding suggests that protective mothering styles may result in configurational memory deficits because of the restrictions such mothering places on pup behavior. Such an interpretation is supported by the results of other studies, using different species. For example, Fairbanks and McGuire (1988) found a relationship between protective mothering styles and subsequent deficits in spatial behavior in vervet monkeys. Monkeys raised by protective mothers were less likely as juveniles to show interest in their external environment (they spent a smaller percentage of their time looking outside their home enclosure and had longer latencies to enter a novel environment) than were monkeys reared by less protective mothers. Mothers were rated on a number of variables designed to assess protective styles, including proximity between mother and infant, restraining of infant by mother, and amount of ventral contact. Furthermore, work with humans found a correlation between restriction of children's exploratory behavior and their later performance on cognitive-intellectual tasks. Several studies have found

that children who were allowed greater freedom to move about the floor of a play area and who had fewer restrictions placed on them by their parents tended to have higher scores on tests of intelligence at later ages (Ainsworth & Bell, 1974; Wachs & Gruen, 1982). In addition, Kagan and Moss (1962) found that protective maternal behavior may play a role in subsequent cognitive deficits.

So, protective mothering may influence development of spatial processing either directly (perhaps by influencing motivation) or indirectly through restriction of early exploration. The results of Experiment 4 suggest that the spatial processing deficit resulted from restrictions in early exploratory behavior. However, the possibility exists that the restricted-rearing group in Experiment 4 failed the allocentric olfactory task for reasons different from those of the liquid-reared animals in Experiment 1. The possibility that two different sets of developmental processes resulted in the same outcome cannot be ruled out by this study.

This study demonstrates that a restriction of experience during a narrow period of development can have specific effects on a general processing system later in life. The restriction occurred during a period when olfaction begins to mediate behavior and the resulting deficit appears to be specific either to the processing of olfactory cues, or to the integration of olfactory and visual cues. These results provide a note of caution: Manipulations of early experience that fail to affect later functioning may do so because of a lack of specificity in the test used to assess that functioning. For example, had this study only examined visual spatial information processing (as in

Experiment 3) a different conclusion about the role of early experience would have been reached. This raises another interesting question. Would hamster pups allowed normal exploratory experience before P14 but restricted exploratory experience after P14 (that is, after the time of eye-opening) exhibit problems with spatial processing of visual but not olfactory cues? If the restriction is modality specific one would expect olfactory processing to be intact, while processing of spatial information provided by visual cues might be attenuated.

The results and conclusions of this study are consistent with the dual memory theory of Sutherland and Rudy (1989; Rudy, personal communication). The restriction of early exploratory experience had a differential effect on the configural associative system (CAS) and the simple associative system (SAS). The allocentric-olfactory tasks of Experiments 1 and 4 required a normally functioning CAS and it was those tasks that the LRG (Experiment 1) and the RRG (Experiment 4) failed. The results of Experiment 2 showed that the SAS (which was sufficient for detecting the spatial change in odor cues in this egocentric version of the task) was not affected by the restricted rearing conditions. Thus, the rearing experience attenuated functioning in the CAS without impairing the SAS. The results raise several interesting questions about the development of the CAS. Since restricted animals were able to detect a change in the configurational relationship of visual cues (Experiment 3) the CAS did function to some extent. Did the early restrictions reduce the number of olfactory projections to neural regions (such as the hippocampus) underlying the CAS? Did these projections form but fail to develop appropriate patterns of

connectivity with post-synaptic cells? Or did the developmental manipulations interfere with the formation of networks involving both olfactory and visual inputs to the CAS? These are questions that can only be addressed by additional research involving a combination of behavioral, physiological, and pharmacological procedures.

On a final, methodological note, it should be pointed out that the procedures used in this study are extremely flexible and offer several advantages for developmental studies of this type. They require no training period and can be conducted in a relatively short period of time. In this study, testing each animal took no more than 75 minutes. This ensures that the animal is at the same developmental stage at the end of testing as at the beginning, which is not the case if training and testing must be spread over several days. The technique allows for various contextual manipulations, so questions about modality-specific and intersensory functioning can be asked. Because habituation occurs in very young animals, the paradigm is ideal for studying the earliest manifestations of spatial processing. Likewise, the paradigm provides a tool for comparing species differences in spatial processing. At present there are very few studies examining the effects of early experience on subsequent spatial processing, although there is an abundance of studies done with adults. The present study offers a procedure and set of starting questions which can guide future investigations of the role of early experience in later spatial processing.

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