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RATS' (*RATTUS NORVEGICUS*) ENCODING AND RETRIEVAL OF SPATIAL AND
NON-SPATIAL ENVIRONMENTAL CUES IN A FORAGING TASK

By

Corrine Nicole Keshen

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NON-SPATIAL ENVIRONMENTAL CUES IN A FORAGING TASK

by

Corrine Nicole Keshen

APPROVED BY:

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Dr. Carlin Miller
Psychology

_____

Dr. Lynda Corkum
Biology

_____

Dr. Jerome Cohen, Advisor
Psychology

May 7, 2013

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ABSTRACT

Animals use various spatial and non-spatial cues when navigating the environment. They can use spatial cues such as a landmark's local position, global position and orientation, or they can use a landmark's non-spatial featural information. The objectives of this thesis were: 1) to determine the conditions under which rats process information separately or simultaneously; 2) to determine how rats process stimuli when previously fixed information becomes more variable; 3) to determine whether animals can use spatial information when a previously encoded non-spatial cue is occasionally eliminated. The results obtained from this research suggest that rats use two different types of processing as a function of variability of redundant information. Moreover, changes within trials were only disruptive for animals that encountered information that had not varied between trials. However, with continued exposure to within-trial changes, these animals' accuracy increased to levels comparable to animals presented with information that varied between trials.

DEDICATION

This thesis is dedicated to my wonderful family who has provided me with endless support and love throughout these past two years.

ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION

<u>Memory</u>

In order to survive, and to ultimately increase the likelihood of survival of its

offspring, an individual must remember certain types of information about a given

environment. These include aspects of its safety; that is, information about predators, and

the quality of food, and what areas (sites) the forager has or has yet to visit. To ensure

that these important events are remembered, an animal must actively use various memory

systems.   Memory has been traditionally categorized based upon different variables, such

as duration (short-term or long-term), subject matter (episodic or procedural) or

application (working memory or reference memory) (Adams-Hunt & Jacobs, 2007).

Animal cognition researchers who study memory, in particular memory for spatial

navigation, are concerned with how animals encode, store, and retrieve information from

working memory or reference memory (Shettleworth, 2010).

Working Memory

Working memory involves the storage and retrieval of information in a particular

situation, and was originally referred to as short-term memory because it is limited in

capacity (Baddeley, 2012). One of the reasons that *working memory* is a more

appropriate term than *short-term memory* is because the organism both manipulates and

can store information until it needs to retrieve it (Baddeley, 1992), rather than simply

holding information for some fixed period of time as the original term implies. Thus

working memory can be considered a more complex operating system than simply short-

term memory. Baddeley and Hitch's (1974) three-component working memory model system consists of the central executive, the phonological loop, and the visuo-spatial sketchpad. The central executive is akin to the nucleus of the system, as it is responsible for deciding what information will be encoded and retrieved, how it will be encoded and retrieved, and also for ultimately integrating the phonological loop and visuo-spatial sketchpad (Baddeley & Hitch, 1974; Baddeley, 2012). The phonological loop is concerned with language, and stores verbal information for a fixed period of time (Baddeley & Hitch, 1974). The role of the visuo-spatial sketchpad in working memory is to provide the animal with mental imagery about the visual and spatial properties of a given environment (Baddeley & Hitch, 1974). Animals can use this mentally represented information for a limited period of time, until they have completed the task that requires this information. Traditionally, researchers studying working memory in animals have been confined to solely studying visuo-spatial working memory, as language is considered to be a uniquely human capacity (Deacon, 1997).

Reference Memory

Reference memory involves remembering information that remains constant overtime (Olton, 1986), and is often used when learning general rules (Frick et al., 1994). Moreover, reference memory is trial independent, as it concerns information that does not change from situation-to-situation (Frick et al., 1994). Reference memory is comparable to long-term memory as it is considered to be unlimited in terms of storage capacity, unlike working memory capacity (Baddeley & Hitch, 1974; Baddeley, 1994; Baddeley, 2012). Moreover, information is constantly exchanged bi-directionally between working and reference memory. Although these two systems operate simultaneously and are in

constant communication, they are fundamentally different in terms of how they process

and store information (Garavan, 1998; Logan & Stadler, 1991). Unlike working memory,

reference memory requires multiple repeated trials for learning to occur (Roberts, 1998).

Moreover, the information acquired by the individual over these repeated trials persists

for an unlimited period of time, unlike information acquired in working memory

(Roberts, 1998). Both working memory and reference memory are widely used terms

that are employed in various disciplines to describe different aspects of memory (Allen et

al., 2012; Arain, Parameswaran & Cohen, 2012; Brissart et al., 2012; David, 2012).

The Physiology of Visuo-spatial Working Memory

Various brain regions have been implicated in visuo-spatial working memory. It

has been proposed that both the prefrontal and parietal cortex play a large role in specific

working memory processes, such as central executive control (van Asselen et al., 2005).

The prefrontal and parietal cortex as a central role in working memory has been proposed

and observed by researchers studying both human and non-human animals. For example,

Friedman and Goldman-Rakic (1994) found prefrontal and parietal cortex activation in

monkeys completing a spatial working memory task. Similar findings have also been

observed in studies examining human visuo-spatial working memory (Constanindis &

Wang, 2004; Jonides et al., 1993; Owen et al., 1998). Although brain regions, such as the

prefrontal cortex and the parietal cortex have been found to be involved in visuo-spatial

working memory, the most implicated brain structure is the hippocampus (Abrahams et

al., 1997; Nelson et al., 2000; O'Keefe & Nadel, 1978; van Asselen et al., 2005). The

hippocampus, which is a structure found in the limbic system, is considered to be

involved in the process of transferring information from working memory to reference

memory, and ultimately facilitating navigation (van Asselen et al., 2005). Moreover, several studies have hippocampal volume to be directly related spatial working memory accuracy. For example, Maguire et al (1999) found that London taxi drivers, who must remember detailed environmental maps, had higher hippocampal volumes than controls subjects. Lee et al. (1998) report that scatter-hoarding birds that must rely heavily on spatial working memory had also higher hippocampal volumes than non-hoarding controls. The rat has been the most widely used study species when studying the role of the hippocampus in memory because of the substantial similarities between the human and rat hippocampus (Anderson et al., 2007). In reviewing this extensive body of research on rats, Anderson et al. (2007) note that damaging the hippocampi does not eradicate prior (pre-morbid) spatial reference memory (e.g. which arms of a radial maze are never baited and which are always baited) but does reduce working memory function (e.g., which arms in the baited set have been or need to be visited in a trial). Such reduction in working memory of course also makes it difficult for the animal to acquire new (post-morbid) reference memory information.

<u>Hoarding Behaviour</u>

When foraging, an animal must process various environmental cues to successfully locate a goal. To find a goal in an environment, an animal must process and remember specific landmarks that it might need to use as beacons. Here, we use the term "beacon" to denote a landmark that is in close proximity to a goal (Spetch & Kelly, 2006). It has been proposed that the way in which mammals and birds cognitively process spatial environmental information when foraging is dependent on their hoarding behaviour (Hampton et al., 2002; Macphail & Bolhuis, 2001; Shettleworth, 2003).

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Animals that scatter hoard may possess different memory capabilities and capacities than animals that either larder hard or do not cache food. Several studies that examined a variety of species have found that hoarding animals use different processing methods than non-storing species (Brodbeck, 1994; Clayton & Krebs, 1994; Jacobs & Shifflett, 1999, Macdonald, 1997; Watanabe, 2005).

Scatter hoarders and Larder hoarders

Scatter-hoarding animals disperse small amounts of food in many widely scattered caches (Daly et al., 1991), whereas larder-hoarding animals collect and hoard a large amount of food in one or a few caches (Daly et al., 1991; De Bruin, 1988). Although both types of hoarding behaviour are strategies used to salvage food from competitors, each provide different benefits and costs: Scatter hoarding requires greater time, as the animal must disperse many small amounts of food widely throughout the environment that puts greater demand on the animal's visuo-spatial working memory (Jacobs, 1992), while reducing risk of pilferage by other foragers. Larder hoarding requires less time to cache food and less demand on the forager's memory to retrieve the stored information, however it increases the risk that a cache will be uncovered and all food will be taken by a competitor or lost through some other environmental catastrophe.

An animal's food-hoarding behaviour can be a valid predictor of how it will encode and retrieve environmental information. Moreover, because different cognitive processes are involved in hoarding behaviour, there may be physiological differences between hoarding animals and non-hoarding animals (Macphail & Bolhuis, 2001). That is, scatter-hoarding behaviour by a species may put greater demand on the hippocampus,

the brain structure implicated in spatial memory, than in non-hoarding animals (Krebs et al., 1989; Sherry et al., 1989). This ecological view, suggesting that cognitive behaviour is species-specific, opposes a general-process view that all animal cognitive activities are governed by the same types of associative learning processes (Bitterman, 2000). Many studies have supported the general process view, by showing that depending upon certain contextual conditions, differences in working memory between hoarding and non-hoarding animals may either be eliminated or changed (Arain & Cohen, in press; Hodgson & Healy, 2005; Herborn et al., 2011; Hurly et al., 2010; LaDage et al., 2009).

Processing Visuo-spatial Stimuli

Cognitive Map Theory

Of interest to researchers who study visuo-spatial working memory, is how environmental information is processed and later retrieved by an animal. It has been proposed that foraging animals encode spatial and non-spatial information as a mental representation that is akin to a cartographic map. This map-like mental representation has been historically referred to as a *cognitive map* (Cartwright & Collett, 1983; Foo et al., 2005; Gallistel, 1990; Gould, 1986; Kitchin, 1994; Jacobs & Schenk, 2003; O'Keefe & Nadal, 1978; Thinus-Blanc, 1988; Tolman, 1948). Tolman (1948) first introduced the notion of a cognitive map to describe "insightful" and "inventive" behaviour observed in rats in search of food by use of routes in foraging tasks. From various experiments assessing food-finding behaviour in the rat, he further postulated that the cognitive map is used by both rats and humans in spatial navigation. Tolman's (1948) cognitive map notion has been widely used to explain the spatial behaviour exhibited by various

organisms, such as humans, rodents, birds and arthropods (Foo et al., 2005; Sheynikhovich et al., 2009; Bingman & Able, 2002; Gould, 1986).

Toman's (1948) original notion of a cognitive map has been extended and modified (Cartwright & Collett, 1983; Gallistel, 1990; Jacobs & Schenk, 2003; O'Keefe & Nadal, 1978; Thinus-Blanc, 1988). For example, Cartwright and Collett (1983) proposed that a cognitive map is composed of various "snapshots" of an animal's environment. Moreover, an animal matches its current environmental experience with a snapshot derived from a greater mental 'library' containing 3-dimensional snapshots of the environment (Bennett, 1996). Traditional unitary cognitive map theories may be able describe how an animal processes information in a somewhat more static environment however; they may have difficulty in describing how the animal processes information in a more highly variable environment (Jacobs & Schenk, 2003).

Parallel Map Theory

Jacobs and Schenk (2003) recognized that there are various environmental cues that influence how an animal will process and utilize environment information when navigating. Rather than having a single unitary map, they proposed the *Parallel Map Theory*: the idea that an animal's cognitive map is comprised of three parallel maps: the bearing map, the sketch map, and the combination of these two maps (Jacobs & Schenk, 2003). The bearing map is constructed by directional cues from the environment and movement cues from the individual. The sketch map involves the processing of specific local landmarks from the environment. Jacobs and Schenk (2003) contended that unlike

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other definitions of the cognitive map, the parallel map theory better accounts for the spatial navigation behaviour of various vertebrate taxa and sex differences within them.

Processing Environmental Stimuli: Separate vs. Simultaneous

Cognitive map theory has been traditionally used to describe how animals encode and retrieve environmental information when foraging (Cartwright & Collett, 1983; Foo et al., 2005; Gallistel, 1990; Gould, 1986; Kitchin, 1994; Jacobs & Schenk, 2003; O'Keefe & Nadal, 1978; Thinus-Blanc, 1988; Tolman, 1948). This theory appears to be valid when describing how an animal would process stable environmental cues; however, in nature, stability is not always the rule. Rather, environments and landmarks within environments are subject to frequent change, and this can potentially influence which resources are available to an animal, as well as how an animal must use available environmental cues. Given these circumstances, it may be more ecologically relevant for an animal to separately rather than simultaneously process environmental cues. This notion further suggests that different types of processing occur under different contextual conditions.

Summary and Objectives

Animals must remember various spatial and non-spatial aspects of an environment when foraging for food. It has been proposed that an animal's hoarding behaviour is a valid predictor of how environmental information will be processed and utilized. It has also been proposed that animals simultaneously process different environmental information and that animal separately process this information (Cartwright & Collett, 1983; Gallistel, 1990; Jacobs & Schenk, 2003; O'Keefe & Nadal,

1978; Thinus-Blanc, 1988; Tolman, 1948). Before one can hypothesize whether the animal's hoarding behaviour will predict how it will process environmental information, or whether animal will process environmental simultaneously or separately, it is important to consider the task at hand, as well as the context of the situation.

There are three objectives of the present study: 1) To determine under which conditions Long-evans rats (*Rattus norvegicus*) process environmental information separately and under which conditions is this information processed simultaneously; 2) To determine how rats process previously fixed information that becomes more variable; 3) To determine whether animals can use spatial information when a previously encoded non-spatial cue is occasionally eliminated.

In a first study, we presented two groups of rats with a segmented-trial foraging preparation. In the 'study' or encoding segment of the trial, the animal obtained sunflower seeds from three object-cued feeders and in the 'test' or memory retrieval segment of the trial, the animal obtained a sunflower seed from the fourth now cued feeder. One group received fixed environmental information between trials and the other group received variable environmental information between trials. We then presented animals with probe trials, where information in the test segment was slightly different than information presented in the study segment. In a second experiment, we presented two groups of rats with the same task, however we gave rats in the fixed group less fixed information, and rats in the varied group more varied information. We then presented rats with three different types of probe trials, which involved presenting rats with different types of information in the test segment of the trial. We also presented rats with probe trials where we eliminated previously encoded environmental cues from the study

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segment. Our experiment provides evidence of a paradigm wherein animals process environmental information differentially, depending on the cues available and the stability of the cues presented.

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CHAPTER 2

UNDER WHICH CONDITIONS DO RATS PROCESS ENVIRONMENTAL
INFORMATION SEPARATELY OR SIMULTANEOUSLY?

<u>Introduction</u>

Spatial navigation is essential for the survival of foraging species (Foo et al.,

2005). To successfully locate food and other necessities in an environment, animals must

learn about the environment's spatial and non-spatial properties. Spatial features include

the local position of proximal beacons or landmarks (their locations in relation to each

other), their global positions (their locations in relation to the distal landmarks at the

perimeter of the environment), and the orientations (their directions from each other)

(Arain et al., 2012). Non-spatial features include the distinct features of these landmarks

or beacons within the environment, such as their colour, shapes, sizes, textures and odors.

Of interest is how these different sources of information about these landmarks or

beacons are remembered and utilized by an organism during foraging expeditions.

Previous research suggests that animals utilize both spatial and non-spatial

information when exploring a given environment. However they use these cues

differentially, and preferentially use certain cues over others (Arain & Cohen, in press;

Brodbeck, 1994). Several factors may determine an animal's preferential cue usage, such

as its species, and possibly it's ecologically derived foraging behaviour. For instance,

certain species, such as the rufous hummingbird (*Selasphorus rufus*), the whiptail lizard

(*Cnemidophorus inornatus*), and the laboratory rat (*Rattus norvegicus*) have been found

to use spatial cues over non-spatial cues (Hurly et al., 2010; Day et al., 2003; Batty et al.,

2009), whereas other species, such as the domestic chick (*Gallus gallus domesticus*), the

goldfish (*Carassius auratus*), and the chimpanzee (*Pan troglodytes*) have been found to preferentially use featural non-spatial information more than spatial information when these cues are segregated (Vallortigara, Zanforlin & Pasti, 1990; Vargas et al., 2004; Kanngiesser & Call, 2010).

An animal's foraging behaviour also may determine its preferential cue usage. Shettleworth (2010) maintains that caching (scatter-hoarding) avian species preferentially use spatial and featural environmental information differently than non-caching avian species. Evidence for such a broad difference was uncovered by two early studies that compared a food-caching avian species to a non-caching avian species (Brodbeck, 1994; Clayton and Krebs, 1994). In those studies, birds were first trained to find one of four feeders that contained inaccessible or partially accessible food during an inspection (study) segment before being allowed to relocate that feeder and remove its food in the test segment after a short retention interval. In post-acquisition non-rewarded probe tests, the arrays of feeders were transformed to dissociate the correct feeder's non-spatial color pattern cues from its correct local (within array) or global (within the larger wall area) position cues over various feeders. These studies found that caching species, black-capped chickadees (*Parus atricapillus*), marsh tits (*Parus palustris*), and jays (*Garulus gandarius*), and non- caching species, dark-eyed juncos (*Junco hyemalis*), blue tits (*Parus caeruleus*), and jackdaws (*Carvus monedula*), were equally accurate in finding the target feeder during regular baseline trials. During non-rewarded probe trials, however, caching birds looked into feeders at correct spatial global and local positions before looking into a feeder with the correct non-spatial cues while the non-storing species showed no specific sequential feeder selection patterns. In a more recent study

(Watanabe, 2005) with only a scatter-hoarding species, western scrub jays (*Aphelocoma californica*), these birds were required to find a baited feeder from a larger array of unbaited feeders. When spatial and non-spatial cues were dissociated, the scrub jays strongly preferred spatial (global and local cues) than featural cues.

Such an ecologically determined predictor of differences in spatial memory has also been found in studies with rodents. For example, Macdonald (1997) presented a scatter-hoarding rodent species, the grey squirrel (*Sciurus carolinensis*), and the native red squirrel (*Sciurus vulgaris*), a species that does not scatter hoard, with a task wherein the animals were required to find artificial food caches. The scatter-hoarding grey squirrel significantly retrieved more caches than the native red squirrel, suggesting that the former possessed better spatial memory than the latter.

Using an animal's ecologically determined foraging behaviour as a predictor of how it processes visuo-spatial working memory information can be problematic, as mixed findings have been reported. For example, Hodgson and Healy (2005) presented great tits (*Parus major*), a non-storing species, with a one-trial associative food-finding task and found that they preferred to use featural cues over spatial cues, and therefore were engaging in hierarchical search. In another study, mountain chickadees (*Poecile gambeli*), a food-caching species, used non-spatial featural information significantly more than spatial information in finding a target object contrary to predictions based on the hoarding model (LaDage et al., 2009). These results are counter to the findings from the earlier previously cited avian research (Brodbeck, 1994; Clayton and Krebs, 1994), as they suggest that food-storing species and non-storing species can both engage in hierarchical search, and have different preferences in different situations.

Given the variability of the results reported, researchers have been prompted to determine whether cue preference is situation-dependent.   Herborn et al., (2011) presented European greenfinches (*Carduelis chloris*) with a foraging task wherein the animals were required to locate a hidden food tray. After having been exposed to the first round of trials, the animals preferred using colour cues over spatial cues, however after repeated exposure to the task, the animals switched to preferring spatial cues. These results suggest that cue preference is context-dependent rather than strictly determined by the birds hoarding predispositions.

In a study conducted by Arain and Cohen (in press), rats (*Rattus norvegicus*) were given a task, which was modified from Brodbeck's (1994) original study. The animals were required to find a target feeder from a configuration of four feeders using spatial and non-spatial information. After animals had first been trained with simultaneously redundant spatial and non-spatial information within each segmented trial but not over trials, they were exposed to probe trials wherein the target object's correct local position; its orientation, its the global position, its non-spatial feature were dissociated over the four cued feeders of a trial's test array. Arain and Cohen (in press) found that rats engaged in hierarchical search for the 'correct' target object by initially selecting one based on its correct non-spatial features and then its correct local position, followed by its correct orientation, and lastly its correct global position. These results are different than the results obtained by Batty et al. (2009), which report that an albino strain of this species (Sprague-Dawley) use spatial information over non-spatial information while foraging. Despite these opposite hierarchical preferences, both studies suggest that they may have been context-dependent cue preferences based in the fact of strain-related and

task-related differences rather than due to any possible differences in their food storing behaviour. Both strains are moderate larder hoarders, but albino Sprague-Dawley rats have considerably poorer visual acuity than hooded rats (Prusky et al., 2002).

Cue usage in foraging is complex, as many variables are important to consider when determining which cue will preferentially be used, when it will be used, and by which species. To determine how a particular individual will utilize environmental cues, it is important to consider how these cues are being encoded by the individual. When foraging, an animal is required to precisely remember which sites it has visited, and which sites it must visit. When an object remains static in an environment, it's local, global, directional and non-spatial properties become part of a consistently redundant representation; however, when an object's location varies over different events, these types of cues will only become a temporarily redundant representation (Arain et al., 2012). To examine how rats encode temporarily redundant spatial features within working memory, Arain et al., (2012) trained rats to retrieve sunflower seeds from three out of four objects in the study segment of a trial, and to find the fourth object, the target object, in the test segment of a segmented-trial. The location of the array was moved between trials, therefore giving the animal separate types of information to encode; however, during this training, the location of the configuration remained fixed within each trial. After successful completion of this phase, rats were then presented with probe trials wherein the location of the array was the same within the trial, as in the previous phase; and probe trials wherein the array was moved to different locations in the test segment. On some trials, identical objects occupied all positions within the three-object study and four-object test arrays to render non-spatial information irrelevant. Moving the

test arrays to different locations initially slightly disrupted rats' accuracy for finding the target object, but later enhanced it, suggesting that the rats had learned when global spatial information became irrelevant and need not be retrieved.

In a second experiment using the same animals, Arain et al. (2012) examined whether rotating the configuration, containing a previously missing object's position in the test segment of a trial produced an enhancement effect, as seen in the first experiment. By rotating the configuration, both types of spatial information (local and global) were sometimes made irrelevant. Rotating the configuration within a trial also initially slightly disrupted the rats' accuracy for finding the target object, but then enhanced it over trials, suggesting that rats were separately encoding and retrieving spatial and non-spatial environmental information (Arain et al., 2012). We note that Arain et al. (2012) never determined whether rats would have simultaneously processed objects' different spatial and non-spatial features had they been fixed over trials, as in that laboratory's earlier research on an enclosed radial maze with proximally-cued arms (Cohen & Bussey, 2005; Tremblay & Cohen, 2007). In those studies, probe tests completely disrupted rats' accuracy for finding a previously blocked arm during a segmented trial, suggesting that rats had simultaneously rather than separately processed these different cues. The question left unanswered by Arain et al. (2012) was whether a similar fixed configuration of non-spatial and spatial cues of an array of beacon objects in the foraging chamber would also have been similarly processed by rats so that within-trial probe test variations would also disrupt their accuracy for finding the target object. Given that the environmental context of a radial maze is vastly different from that of a foraging arena, we consider that an answer to this question must be empirically

determined. Therefore we designed the present study to answer it as follows: Instead of using only a within-subjects design, we added a between-subjects factor by presenting two different groups of rats, a varied and a fixed configuration group, a segmented-trial, consisting of a three-object study segment and a four-object test segment. The varied configuration group received similar training as the rats in the Arain et al. (2012) study. The fixed configuration group received the same configuration in the same location between trials. In the study segment, the animal had to open the three object-cued feeders to obtain a sunflower seed under each object, and in the test segment, the animal had to open the correct fourth feeder to obtain a seed under the previously missing object. Following this training, rats received occasional probe trials with a rotated array. We hypothesized that rats in the fixed group would process environmental cues simultaneously, and that rats in the varied group would process this each type of spatial and non-spatial information about objects in the study arrays separately. We predicted that rats in the fixed group should complete the training phase earlier than the rats in the varied group, as they have static information to encode. This prediction is based on traditional association theories proposed by Rescorla and Wagner (1972) and Pearce (1987). We also predicted that rats in the varied group would find the target object more accurately on probe trials than rats in the fixed group.

Method

Subjects:

Twelve male hooded-rats (*Rattus norvegicus*) of the Long-Evans strain were used in the present study. They were obtained from Charles River Breeding Farms in St.

Constant, Quebec, weighed an average of 350 g upon arrival, and began the experiment at four months of age. The rats were placed on an *ad lib*. food and water schedule for several days after their arrival, after which they were put on a food deprivation schedule, which involved reducing their weights to approximately 90% of their free-feeding weights. The rats were fed 20-25 g of Prolab® RMH 3000 rat chow and 300 ml of water for 2 hours in standard stainless steel individual holding cages after each experimental session. Following feeding, the rats were returned to their group cages, each which housed four rats, in the colony room. Rats received water *ad lib* in the group cages and individual holding cages. The colony room was maintained on a 12/12h dark light cycle, where room illumination was slowly changed over a 30 sec. period at the start of each light or dark cycle. An experimental session always began within 2 h of the beginning of the dark cycle. Although rats have been found to spend 76.8% of a 24-hour period in sleep, they are most active at night (Clancy et al., 1978). During this study, two batches of six rats were run in succession.

Apparatus and Materials:

We used the same foraging arena from Arain et al. (2012) in the present study (see Figure 1). The arena consisted of a 1.2 m square-shaped aluminum foraging platform that stood 56 cm above the floor of the experimental room. The arena was enclosed by 46 cm high wooden walls, which were painted grey. A black curtain suspended from the ceiling surrounded the walls. A small guillotine door that was positioned in the center of each wall but only that on the south wall led to a standard stainless steel individual holding chamber. Only that door could be opened or closed by the experimenter manipulating it with a string and pulley system. The experimenter

could observe and record the rat's behaviour inside of the arena on a PC laptop monitor connected to a web camera located 1 m above the south wall. This configuration allowed the experimenter to remain out of sight from the rat in the apparatus while obtaining a birds-eye view of its foraging activity.

The floor of the arena contained 25 holes arranged in a 5 by 5 grid with 20.3 cm between each hole. Each hole could be filled with a foraging feeder or with a metal cylinder cover to block the hole (Figure 2). The foraging feeders were made from a rectangular block of aluminum, which measured 16.5 cm by 7.6 cm by 2.5 cm. The feeder contained a small horizontally sliding metal plate with a semi-circular concave end that the rat could push with its nose to slide the cover off a shallow indented food well to retrieve a reward of an unsalted roaster sunflower seed (Figure 3). Each food well also contained a perforated metal floor under which was packed inaccessible seeds (Figure 4). Thus any unbaited food wells contained the same sunflower-seed odor as did the baited ones. A small magnet was embedded into the center of the sliding metal plate to allow the experimenter to easily attach and remove objects that had a metal flat-head screw in their base. A total of five different junk objects, each with a height of approximately 6.3 cm, were used in this experiment (Figure 5): a green Lego cube, a hollow metal circle, a plastic spool, a seashell, and a metallic spring. Four replicates of each object were used as will be described in the procedure section (Figure 6).

Procedure:

Pretraining:

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Each rat was initially trained to open the foraging feeders and received two trials, each lasting a maximum of 10 minutes, for a total of two months. Eight foraging feeders were randomly dispersed throughout the arena. Four of the feeders, each with a different orientation, had an object atop of it. The other four feeders, each with a different orientation, did not have an object. All of the feeders were fully opened, exposing the circular food cup. Each of the four object-cued feeders was baited with six sunflower seeds on its food well's perforated floor, but feeders without objects had no seeds on their food well floors even though both sets of feeders contained seeds beneath their respective food well floors. The objects were randomly selected on each trial.

Each animal was initially placed inside the arena and was permitted to explore and eat the sunflower seeds for a maximum time of 10 minutes. Following the 10 minutes, the animal was removed from the apparatus and was placed inside an individual cage outside the experimental room where it received *ad lib.* water. The location of the foraging feeders varied from trial to trial, as did the objects.

A basic shaping paradigm was used to teach the rats to open the foraging feeders: The rats were initially presented with fully open feeders containing accessible seeds. From trial to trial, the feeder became slightly more closed in small increments, until the animal was presented with a completely closed feeder that they would have to push open in order to obtain a seed. The number of seeds present in the feeder was also gradually decreased until each feeder with an object contained solely one seed. Criterion was reached when a rat opened four fully closed object-cued feeders within five minutes of being in the foraging arena. The four feeders without objects were left completely open and were not baited with accessible sunflower seeds. After the animal had reached

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criterion, it was placed in the start box at the beginning of each trial and was removed from the start box at the end of each trial. The shaping technique that was used is analogous to shaping techniques developed by Skinner (1953) where animals learn to gradually approach and press a lever for food pellets.

The twelve rats were run in two successive batches of six rats each. Only after the first batch had completely finished this experiment was the second batch run. In other words, after the first six animals had completed the experiment, we replicated it with the remaining six rats with the following change in pretraining procedures. Each rat in the first batch underwent one pretraining trial per day for approximately two months but each rat in the second batch underwent two pretraining trials per day for approximately two months. This difference in procedure was carried out to promote acquisition of actual segmented trial (missing object recognition task) in the second batch of rats as will be discussed later in this chapter.

Training:

Each rat was assigned a specific configuration and four objects. Rats were presented with the same configuration and the same objects for the entire experiment. A configuration was composed of four feeders in a specific formation, with each feeder placed in a different orientation (see Figure 7). The rats were also randomly assigned to one of two groups: the fixed group or the varied group.

After a rat had reached criterion for the pretraining phase, it was then moved onto the training phase. The training phase consisted of presenting each animal with a segmented trial that was composed of a study segment and a test segment. In the study

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segment of a trial, the rat was presented with its assigned configuration in the foraging arena. Three of the four feeders would contain an object and the fourth remaining feeder had no object. After the rat had opened the three feeders with objects, the rat was removed from the arena and was placed in a plastic holding cage underneath the foraging apparatus for a 2-minute inter-segment interval (ISI). During the ISI, the arena and the foraging feeders were cleaned with an antibacterial cleaning solution, and the feeders were repositioned for the test segment of the trial. Following the 2-minute ISI, the rat was placed back into the foraging arena through the start box and was presented with the test segment of the trial. The test segment consisted of four feeders, in the same configuration and in the same location as the study segment, however the fourth missing object from the study segment was now present, and was placed atop the fourth feeder. The fourth feeder previously not cued by an object was now the only feeder that contained an accessible seed. Once the animal opened the correct feeder, it was removed from the apparatus and placed inside it's individual cage and was given water. If the rat did not complete the task within 3 minutes, it was removed from the apparatus, and the trial was not used for analysis. During this phase, each rat received two distrusted training segmented trials per day. Only after all rats had completed their first training trials could they be run on their second trial. Over days the sequence that rats ran on these trials also varied so that no rat ever ran its trials at the same times consistently during this and on the following phases. These procedures kept inter-trial intervals within a session at approximately 2 h.

To control for odor cues, the arena and the feeders were cleaned with an antibacterial disinfectant during the ISI and after each trial. Replicates of each object were also used and feeders were also switched.

For rats in the fixed group, the location of the configuration in the arena remained constant from trial to trial, as did the relative position of the feeder objects. For rats in the varied group, the location of the study and test arrays and the positions of objects within these arrays varied over trials but not between any trial's study and test segment (see Figure 8). Criterion for moving on to the probe trial section of the experiment was when a rat had opened the correct feeder in the test segment on 9 out of 12 training trials. The six rats in the first part experiment required a considerable number of trials to criterion, between 51 and 62 training trials. We note that rats in two earlier studies (Arain et al., 2012; Arain et al., in press) had reached this criterion in far fewer trials. A main difference between this and the earlier experiment is that rats in the former received two pretraining trials rather than one pretraining trial per session. Therefore we gave the second batch of six rats two pretraining trials per session to possibly promote faster acquisition during this training phase. We note that this batch only needed between 14- and 20 training trials to reach criterion before they could receive probe trials.

Probe Trials:

The term "probe trial" was first introduced by Guttman and Kalish (1956) to denote a specific occasional trial interspaced among regular (baseline) trials that tests what the animal has learned on baseline trials. This technique was originally applied in free-operant discrimination research on stimulus generalization tests with pigeons. Probe

trial is now a commonly used term in any kind of discrimination task in experimental

psychology. Following completion of the training segment of the experiment, rats were

given probe trials interspersed among regular training trials. One out of every three trials

was a probe trial. The trial selected to be a probe trial was randomly determined with the

restriction that no back-to-back probe trials would occur over sessions. Each probe trial

was composed of two segments, as in the training trial. The study segment of the probe

trial was identical to that of a training trial: The rat was placed into the apparatus and was

required to open the three feeders with objects. The configuration was the same, as in the

training trials. Following completion of the study segment, rats were removed from the

arena for 2 minutes. During the ISI, the arena and feeders were cleaned with antibacterial

solvent, and the feeders were rearranged. Following the 2-minute ISI, the rat was placed

back into the arena and was presented with the test segment: The configuration remained

the same and was in the same location, however the configuration was rotated either 90°,

180° or 270°, therefore sometimes making the global position and the orientation of the

correct feeder irrelevant. Rats were given a total of 12 probe trials with each probe trial

consisting of a different rotation.

Statistical Analyses:

Two 2 between-subjects (fixed group vs. varied group) x 2 within-subjects

(baseline trial vs. probe trial) repeated-measures ANOVAs were conducted to determine

whether groups differed in locating the target feeder. The repeated-measures feature of

this design permitted the use of a small number of rats (n=6) in each group without

sacrificing statistical power for uncovering 'true' differences. We note that the power

calculated from all tests in this and the following experiment was never below .78. The

first ANOVA was conducted to examine whether the two groups of rats differed in terms of their first choice accuracy on baseline and probe trials. The second ANOVA was conducted to examine these differences for second choice accuracy. Moreover, post-hoc independent samples t-tests were conducted to further examine the nature of these group differences.

Results

Probe Trials:

Figure 9 shows fixed and varied group performance for finding the target feeder on the first choice and by the second choice on probe trials. As seen in this figure, rotating the configuration decreased the fixed group's performance to near chance; however it increased the accuracy of the varied group. These differences produced a significant interaction under both conditions for both measures of accuracy, $F_{1,10} = 49.37$, $p < 0.01$, $F_{1,10} = 45.12$, $p < 0.01$. Separate ANOVAs for trial-type within each group revealed that the decline in performance for animals in the fixed group was significant under either measure, $F_{1,5} = 100.84$, $p < 0.01$, $F_{1,5} = 39.33$, $p < 0.001$. The observed increase in accuracy for the varied group on the first choice failed to reach significance, $F_{1,5} = 3.42$, $p = 0.12$, but was significant by the second choice, $F_{1,5} = 13.21$, $p = 0.02$. We note that rotating the array improved first choice accuracy for four rats and decreased it it for the other two rats in the varied group but increased every rat's accuracy for finding the missing object by the second choice in this group. Further analyses carried out with independent-samples t-tests revealed that on the first choice, the fixed group's performance was superior to the varied group's performance on baseline trials (non-

rotated), but was significantly poorer than varied group performance on rotated probe trials, , $t_{10} = 2.20$, p = 0.05, $t_{10} = 5.40$, p < 0.01. By the second choice, the difference between groups on the non-rotated baseline trials was not significant, however rotating the array produced significantly poorer performance for the fixed group, $t_{10} = 3.32$, p < 0.01. Figure 10 shows the fixed and varied group's accuracy in locating the target feeder throughout three blocks of four trials. As seen in the figure, there was no difference in each group's performance throughout each block of trials, however, the varied group's performance was significantly more accurate than the fixed group's performance $F_{1,10} = 28.00$, p < 0.001.

Discussion:

We examined the accuracy of two groups of rats in finding a target object using relevant environmental cues. The fixed group received the same configuration, in the same location, and objects with the same relative position between trials, whereas the varied group received the same configuration, in a different location, and objects with a different relative position between trials. We predicted that rats in the fixed group would acquire the initial task faster than rats in the varied group, as they were presented with static information between trials. This prediction is based on traditional association learning theories (e.g., Rescorla and Wagner, 1972; Pearce, 1987; 1994). Rescorla and Wagner proposed a mathematical formulation to account for how distinctly different cues could be combined as a compound cue, and that its association would be greater than either of its separate components. Pearce (1987, 1994) maintained that such cues presented simultaneously result in a unitary representation and that an organism will associate these combined cues with a reinforcer. Because we had variation in terms of

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how many training trials rats in the first part of the experiment received in comparison to rats in the replication of the experiment, we could not conduct proper statistical analyses to test this hypothesis. Although we are uncertain as to whether rats in the fixed group acquired the training task significantly faster than rats in the varied group, we did find that in both parts of the experiment, rats in the fixed group graduated from training earlier than rats in the varied group. The second group of six animals that were used in this experiment completed the training phase in fewer trials than the first group of six animals. We gave the second group more overall pretraining trials. Perhaps the extra pretraining these animals received aided them in acquiring the segmented trial task during the training phase. We also decided to give the rats in the second part of the experiment a maximum of 20 trials before presenting them with probe trials, as we felt that there accuracy at finding the target object was much higher than the first group of rats at that stage.

Our prediction that rats in the varied group would be more accurate than the fixed group in finding a target object when the configuration was rotated either 90°, 180° or 270° was supported by our results. These results suggest that different types of processing occur, depending on how the environmental stimuli are presented to an animal. Moreover, when presented with the same task, the way in which information is processed will greatly influence the animal's accuracy. We found that rats in the fixed group were simultaneously processing environmental cues, as their performance significantly decreased when they were presented with a slightly different environment. We also found that rats in the varied group were individually processing environmental cues, as their performance did not decrease when they were presented with probe trials

wherein environmental information changed. These results support our hypothesis that environmental conditions influence whether a rat will process stimuli simultaneously or individually.

The foraging feeders that were used in this study were modified from those in the Arain and Cohen (in press) study so that both baited and unbaited feeders could be opened. In the earlier study, rats may have been able, in some way, to distinguish a locked from an unlocked feeder that could have considerably helped them master the task. Instead of using two types of feeders, we baited one type of feeder with sunflower seeds, however all feeders had inaccessible seeds under their perforated metal plates. The animals in our experiment took approximately two months to complete the pretraining phase, whereas the animals in the Arain and Cohen study only needed two weeks of pretraining. Perhaps our animals had more difficulty sliding the food well covers off the food wells in our modified feeders given the shallowness of the wells with the floor caps.

When we rotated the configuration during the test segment of the probe trials, certain types of spatial information were made irrelevant, therefore the animal could only use non-spatial featural information, the local position of the correct feeder, and at times the global position. The global position was either irrelevant or relevant, depending on the type of rotation. One could argue that the animal was not given a strong enough sense of direction, as the walls of the apparatus were identical, and each wall contained the same guillotine-style door. This problem was eliminated in the next experiment.

The results obtained from the present study support the notion that the rats in the Arain and Cohen (2012) study were separately processing spatial and non-spatial environmental cues, however they extend their findings, by suggesting that how an animal processes information is dependent on the task at hand. Our experiment demonstrates that there are two context-specific ways for processing multiple sources of information in our foraging arena object recognition task, as there seemed to be in the radial maze from the Tremblay and Cohen (2005) study. By adding a fixed group that was presented with environmental information that remained static, it is apparent that a different type of stimuli processing occurred, as the animals had a significantly more difficult time accurately finding the target object on probe trials. These findings support the context-dependent hypothesis proposed by Herborn, Alexander and Arnold (2011), and provide a good example of differential processing. Our results suggest that when the landmarks within an environment are rendered fixed, an animal processes this information simultaneously to ultimately forage efficiently. We see a different type of processing when the features of an environment are constantly varying: When landmarks in an environment are not stable, an animal processes each type of information separately, and this helps the animal adapt to these changes, ultimately foraging more effectively.

The results obtained from this experiment are useful for conducting comparative studies across different species. Our results extend the idea of how working memory functions differently under different contexts and this can be applied to the study of comparative cognition. Future research should examine sex-based differences. The subjects used in this experiment were males, and it has been proposed that males and

females process information differently, and use this information differently when foraging (Barkley & Jacobs, 2007). Future research should also take into account how static environmental cues must be in order for simultaneous processing to occur. We address this suggestion in our next experiment.

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Figure 1: The foraging arena, which is composed of 25 holes filled with removable metal cylinders and four foraging feeders. This picture was obtained from Arain & Cohen's (in press) research.
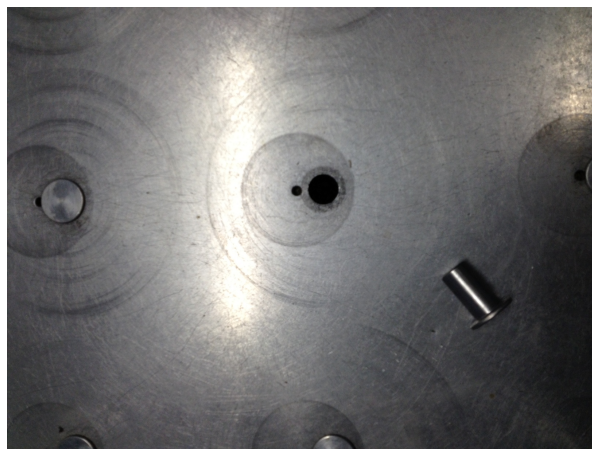

Figure 2: An empty hole in the foraging arena that can be filled with a metal cylinder, as seen on the right, or a foraging feeder.
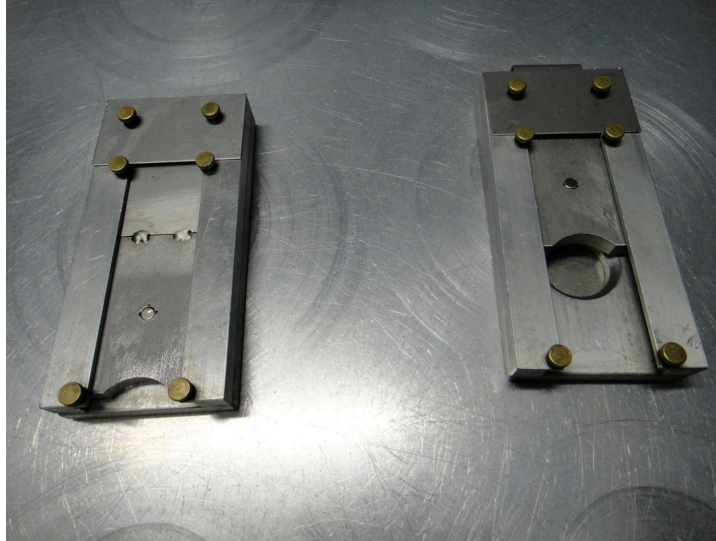
Figure 3: Foraging feeders, as they would appear closed (left) and open (right). This image was taken from Arain and Cohen's (in press) study.
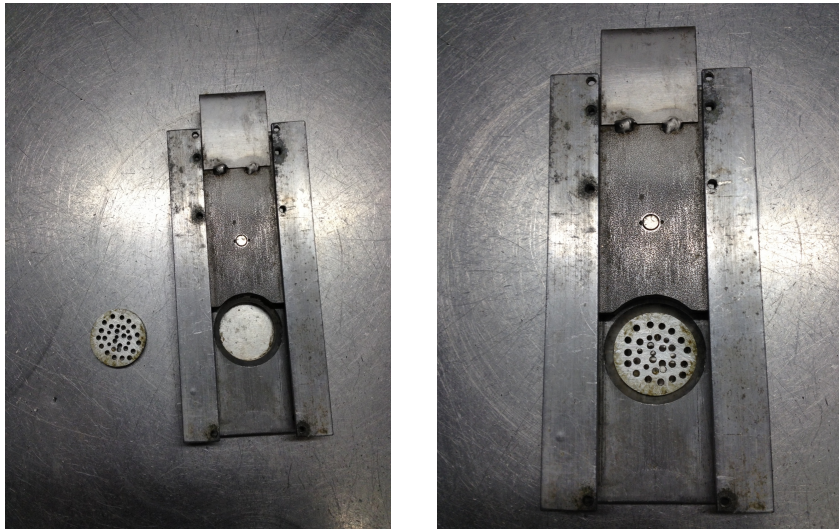

Figure 4: The feeder on the left is open and contains no perforated plate. Also seen in the image on the left is the metallic plate that can be inserted into the open cup to render seeds inaccessible. Pictured on the right is on opened foraging with an inserted perforated metallic plate.

Figure 5: The objects used in this experiment.

Figure 6: A closed foraging feeder with an object atop of it.

Figure 7: The layout of the four configurations. Each animal was assigned one of these configurations. The arrows indicate the direction that the feeder opened.

Figure 8: The layout of configurations, as they would appear from the study segment of one trial (top) to the next trial (bottom). The two figures on the right represent two trials for a rat in the fixed group, and the two figures on the left represent two trials as they would appear for a rat in the varied group.

Target Object Found
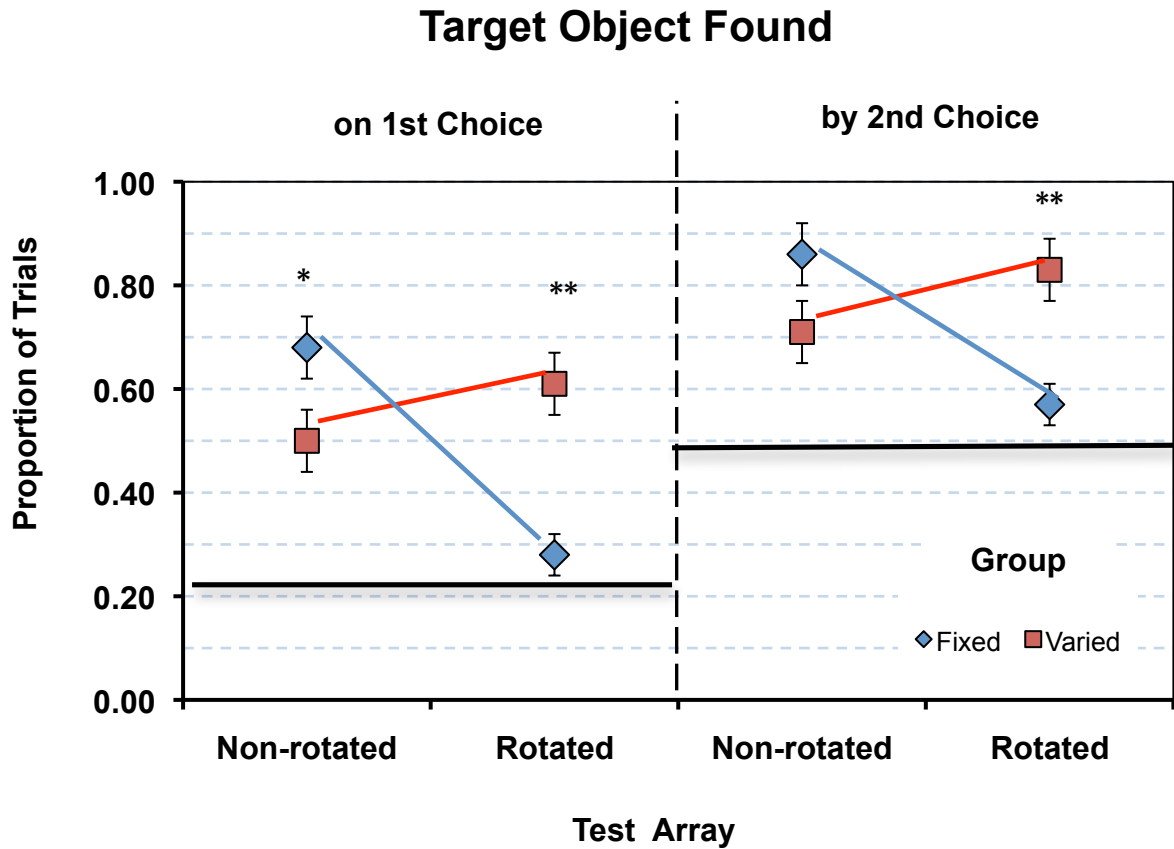
Figure 9: Proportion of trials rats found the correct feeder on their first and second choice in the test segment of baseline (non-rotated) and probe (rotated) trials. The solid line going across each graph represents chance.

Accuracy in Locating the Target Feeder on Probe Trials
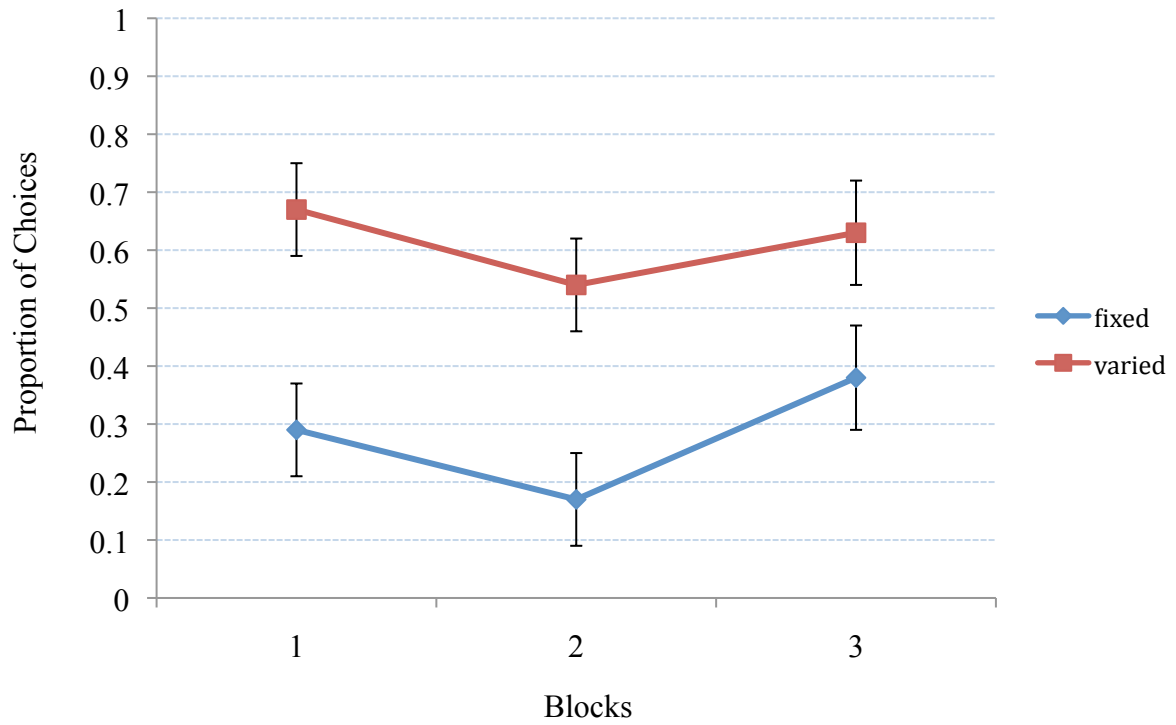
Figure 10: Rats' accuracy in finding the target feeder on probe trials during blocks of four trials. Both fixed and varied groups' performance is broken down into three blocks of four trials.

CHAPTER 3

DOES DIFFERENTIAL PROCESSING OCCUR WHEN ENVIRONMENTAL
CONDITIONS ARE RENDERED MORE VARIED BETWEEN TRIALS?

<u>Introduction</u>

While foraging, animals must consider various aspects about the environment and landmarks within the environment. Previous research has proposed that animals simultaneously process different environmental information; however, it has also been proposed that environmental information is separately processed (Cartwright & Collett, 1983; Gallistel, 1990; Jacobs & Schenk, 2003; O'Keefe & Nadal, 1978; Thinus-Blanc, 1988; Tolman, 1948). Recent literature has placed large emphasis on the notion of context-dependency, suggesting that different types of memory processes can occur under different circumstances or situations (Herborn et al., 2011). The research that was discussed in Chapter 2 suggests that different sources of information can be processed either simultaneously or separately depending on how they are presented to the animal. Our paradigm for assessing rats' object recognition from their visuo-spatial working memory is a valid method for determining which type of information processing is being used. In the previous experiment, we found that rats processed spatial and non-spatial cues simultaneously when both types of cues occurred in a fixed configuration over trials, but processed them separately when they varied over trials.

Jacobs and Schenk's (2003) Parallel Map Theory recognizes orientation as a highly important environmental cue. The Parallel Map Theory proposes that animals encode and construct internal maps based on directional cues from the environment. Together with information from environmental landmarks, directionality aids the animal

in constructing cognitive maps (Chai & Jacobs, 2009; Jacobs & Schenk, 2003). The experiment discussed in Chapter 2 provided the animal with four types of environmental information of objects within an array: 1) their relative local positions, 2) their global position within a larger environment, 3) their orientations, 4) their non-spatial features. In this experiment, the only sense of orientation that the animal could use was the actual position of the feeders, their relative orientations, within the foraging arena, as the walls enclosing the arena were identical. In order to give the animals a greater sense of absolute orientation, we added three distinct panels to three of the walls within the arena. By adding this feature to our paradigm, the animal is able to use direction in this task.

Previous research conducted in our lab, involved presenting rats with a hierarchical search task: Rats (*Rattus norvegicus*) were presented with a standard segmented-trial task, wherein the study segment they were required to retrieve sunflower seeds from three feeders containing objects, and in the test segment, they were required to retrieve a sunflower seed from the fourth feeder containing the missing object (Arain & Cohen, in press). Following training, rats were presented with segmented probe trials: In the test segment of a probe trial, the non-spatial and spatial cues were dissociated, so that each feeder represented a specific cue (local, global, orientation, object), as in the Brodbeck (1994) study. However, unlike the results obtained from Brodbeck's research, Arain and Cohen found that rats selected the feeder representing non-spatial information, followed by the feeder representing the correct local position, followed by the correct orientation, and lastly its global position.

When examining cue preference, mixed findings have been reported. Moreover, with some tasks, certain animals, such as mammals and birds, have been reported to

preferentially use non-spatial cues over spatial cues, and on other tasks these species preferentially use spatial cues over non-spatial cues (Brodbeck, 1994; Hodgson & Healy, 2005; LaDage et al., 2009). Previous studies examining cue preference in rats has found that rats use spatial environmental information over non-spatial featural cues when locating a target (Batty et al., 2009; Cheng, 1986; Hayward et al., 2003; Pearce et al., 2001). However, Arain and Cohen (in press) observed that rats preferentially used non-spatial cues when presented with a task that is used in the present study. Given these findings, it is reasonable to assume that by using our research paradigm, rats would preferentially use objects' non-spatial information more than their spatial information to complete a task.

We found that rats processed environmental stimuli differently, depending on how that information was presented. The present study extends the research that we presented in Chapter 2. We divided rats into two groups: a fixed group and a varied group, as in the previous experiment. Rats in the fixed group received the same configuration in the same location and the same relative position of objects, from trial-to-trial, as in the previous study; however, they received more varied information by being exposed to rotating configurations of 90°, 180° or 270° between trials. Thus each object's relative position and orientation but not its global position within the array remained the same over trials   Rats in the varied group received the same rotating configurations in a different location with different object-relative positions between trials. Thus, unlike rats in this group in the first experiment, their geometrical array configuration also was rotated over trials. We decided to present the animals with more variable information to see whether this would influence how they processed and used environmental

information either simultaneously for the fixed group or separately for the varied group, Following completion of the training phase rats in both groups were presented with three different types of probe trials: 1) a within-trial rotation probe trial wherein the geometrical configuration was rotated in a probe trial's test segment from that in its study segment, 2) a within-trial location probe trial wherein the array was relocated from the study segment to the test segment, 3) a within-trial combination array rotation and location probe trial where the configuration was both rotated and relocated in the test segment of a trial. Rats were also given identical object probe trials, wherein all objects in the test segment were identical, therefore eliminating the non-spatial information as a relevant cue.

We hypothesized that rats in the fixed group would continue to process information simultaneously and that rats in the varied group would continue to process information separately. We also hypothesized that occasionally eliminating a previously encoded non-spatial cue, would disrupt fixed rats' accuracy for locating the trial's previously non-baited feeder. Based on results from our the Chapter 2 study, and based on traditional association theories (Pearce, 1987,1994; Rescorla & Wagner, 1972) we predicted that rats in the fixed group should complete the training phase earlier than rats in the varied group. We also predicted that rats in the varied group would have higher accuracy when finding the target feeder on regular probe trials than rats in the fixed group. Moreover, we predicted that rats in the fixed group would have greater difficulty selecting the target feeder on identical object probe trials than rats in the varied group. These predictions were based on findings from the Chapter 2 experiment. These results will extend our previous findings by determining whether differential processing occurs

when the environmental information is made slightly more variable and how well animals can process only spatial information.

Method

Subjects:

Twelve experimentally-naïve male Long-Evans hooded rats purchased from Charles River, Quebec, as in the previous experiment, were divided into two batches of six animals in this experiment. We ran one batch of rats before running the second batch, as in the experiment discussed in Chapter 2 for logistical reasons.

Apparatus and Materials:

We used the same objects and foraging chamber from the previous experiment. We modified the foraging chamber by inserting 1.2 m of Masonite panels onto three of the four arena walls. Each panel was visually distinct: the panel on the east wall was solid blue, the panel on the north wall was solid white, and the panel on the west wall contained seven blue and white vertical stripes. The wall containing the start chamber remained the same as in the previous experiment. The other three distinctly different walls served to provide rats with fixed distal directional cues. We also modified the feeders by removing the double-chambered food chamber and inserting a locking mechanism, a pin beneath the food cup cover that prevented the rat from completely moving the cover off of the food cup to make seeds inaccessible. For the sake of simplicity, we label any locked and unlocked feeder as non-baited and baited, respectively. This feeder modification insured that "baited" and non-baited feeders contained the same amount of seeds to control for olfactory cues. We also discovered

that this modification allowed rats to more easily move the food cup covers, as described in the following section.

Procedure:

<u>*Pre-training Phase:*</u>

The rats received the same initial pre-training procedures, as given to rats in the first experiment. We note that rats in the present experiment learned to open closed feeders more rapidly than rats in the previous experiments. Both groups of rats from this experiment successfully completed the pre-training phase of this experiment within two weeks.

<u>*Training Phase:*</u>

Each rat was assigned a specific configuration and four objects. The rats were also assigned to either the fixed or varied group. As in the first experiment, each rat received the same configuration and the same objects from trial to trial.

The training phase from this experiment consisted of segmented trials, which were composed of the study and test segments, as in the first experiment. The same procedure was followed, with some modifications as follows. For rats in the fixed group, the same array configuration was presented in the same location from trial to trial with the same object-relative positions. For rats in the varied group, the same configuration was presented in a different location from trial to trial with varying object relative position. The difference between the training trials in the current experiment and in the previous experiment was that in this study, both groups of rats received 90°, 180° and

270° rotations of their specific array configurations between trials. The configuration rotation for each trial was randomly determined, ensuring that each rat received a nearly equal distribution of each rotation.

After a rat had reached criterion of opening the correct feeder in the test segment on 9/12 trials, or it had reached 20 trials, whichever came first, it received the probe trial phase of the experiment. The first batch of rats required between 11 and 20 training trials and the second batch required between 13 and 20 training trials before being placed onto the probe trial phase.

Experiment 2A:

After reaching criterion or completing 20 training trials, rats were presented with probe trials. As in the experiment in Chapter 2, one out of every three trials was a probe trial, whereas the other two trials training trials. No probe trials were presented consecutively, and the trial selected to be a probe trial was randomly determined.

The structure of a probe trial was the same as the structure of a training trial: each probe trial was constructed of two segments: a study segment and a test segment. We presented the rats with three different probe trials. The study segment of all probe trials was the same as the study segment of a training trial: Each rat was presented with its configuration and its objects. One of the feeders was locked and contained no object. The test segment of each probe trial differentiated one type of probe from another type. In the test segment of a *Rotation* probe trial, the configuration presented in the study segment of the probe was rotated 90° or 180° or 270°. This type of probe trial was the same as the probe trials in the first experiment in that the correct feeder now contained

the missing object from the study segment in the same relative position within the array but in a slightly different global location within the arean. In the test segment of a *Location* probe trial, the configuration from the study segment of the trial was relocated to a different part of the arena so that only the global information of the correct feeder was made irrelevant but its absolute within array position remained unchanged. In the test segment of a *Combination* probe trial, the configuration from the study segment of the trial was rotated 90°, 180° or 270° and was relocated to another part of the arena. Thus both the absolute local and global spatial features of the missing object became irrelevant but its relative spatial position remained relevant. Rats were given six presentations of each probe trial, for a total of 18 probe trials before being presented with identical object probe trials.

Experiment 2B:

After a rat had completed 18 probe trials, it was then presented with identical-object probe trials. An identical objects probe trial occurred one out of every three trials, as did the regular probe trials. Moreover, one out of every three probe trials was an identical-object probe trial, therefore in Experiment 2B, rats received a total of 18 probe trials, composed of six identical object probes, and twelve different object probes. There were two types of identical object probe trials that we presented to the rats: In a *missing-object replicate* probe trial, the study and test segment were the same as in a typical probe trial, however in the test segment, instead of simply adding the missing object onto the correct feeder, all of the feeders contained replicates of the missing object, therefore making the non-spatial information redundant. The second type of probe trial, the *object replicate* probe trial, was identical to the missing-object replicate probe trial, however the

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replicates in the test segment of the trial were one of the objects that the rat encountered in the study segment of that trial.

Rats were each given a rotation probe trials, a location probe trial and a combination probe trial, under each identical object condition, to receive a total of six replicate probe trials.

Statistical Analyses:

Independent samples t-tests were conducted to examine whether there were differences between the fixed and varied group, in terms of reaching criterion for completing the training phase. Two 2 between-subjects (fixed group vs. varied group) x 2 within-subjects (baseline vs. probe trial) x 3 within-subjects (rotation probe, location probe, combination probe) ANOVAS were conducted to examine whether there were any significant differences between groups on first choice accuracy and second choice accuracy. Moreover, we conducted independent samples t-tests to examine group differences on each type of probe trial, and paired samples t-tests to examine group differences for block performances. A 2 between-subjects (fixed vs. varied) x 2 within-subjects (baseline vs. probe trial) x 2 within-subjects (study segment object vs. missing object) x 3 within-subjects (rotation probe, location probe, combination probe) between subjects ANOVA was conducted to examine group differences on identical object probe trials. Moreover, we conducted independent samples t-tests to examine group differences on each type of probe trial.

Results

Training

Figure 11 shows the mean number of trials each group needed to reach acquisition criterion. As seen in this figure, we found that rats in the fixed group required substantially more trials to reach criterion than rats in the varied group. An independent groups t-test revealed this difference to be significant, $t_{10} = 3.34$, p < 0.01. Figure 12 shows the proportion of rats in each group selecting the target feeder on acquisition training trials. As seen in the figure, there is no difference between groups in terms of selecting the target feeder on the first, or on the second choice.

Experiment 2A

We examined whether there were differences between the fixed and varied group, in terms of test segment accuracy for finding the correct feeder under probe conditions. Each rat's test performance from each trial preceding a probe trial, its baseline performance, was noted, along with its accuracy for finding the correct feeder in the test segment of the probe trial. Figure 13 shows both groups' accuracy in locating the target object by the first choice. As seen in this figure, changing the array's position in the test segment of a probe trial produced a significant interaction between trial type (baseline vs. probe) and probe type (rotation, location and combination), $F_{1,20} = 8.51$, p < 0.01, and a significant interaction between trial type (baseline vs. probe), probe type (rotation, location and combination), and group (fixed vs. varied), $F_{1,20} = 3.83$, p < 0.05. In Figure 13, we see a decline in performance on rotation and combination probe trials for both groups, however we see an increase in location probe trials. A separate ANOVA for trial-type within each group revealed that the decline in performance for animals in the fixed group was significant from baseline to probe trials, $F_{1,10} = 43.39$, p < 0.01, however no such difference was found for rats in the varied group, $F_{1,10} = 1.87$, p = 0.24. As seen

in Figure 13, there is a significant difference between the two group's performances on rotation probe trials, $t_{10} = 2.28$, $p < 0.05$, with the varied group having greater accuracy than the fixed group. Also seen in Figure 13, there is a significant difference between the two group's performances on combination probe trials, $t_{10} = 6.04$, $p < 0.01$. Figure 13 displays no differences between the group's performances on location probe trials.

Both groups' accuracy in locating the target object by the second choice is seen in Figure 14. As seen in this Figure, changing the array's position in the test segment of a probe trial produced a significant interaction between trial type (baseline and probe) and probe type (rotation, location and combination), $F_{2,20} = 14.53$, $p < 0.01$, and between trial, type, probe type, and group (fixed vs. varied), $F_{2,20} = 8.51$, $p < 0.01$. Figure 14 shows no significant group differences between rotation and location probe trials. A separate ANOVA for trial-type within each group revealed that the decline in performance for animals in the fixed group was significant, $F_{1,10} = 16.13$, $p < 0.01$. Figure 14 also shows that rat in the varied group had no significant change in their accuracy for finding the target object by the second choice from the baseline trials to the probe trials. It should be noted that rats in each group continued to perform probe trials significantly above chance levels under each accuracy measure.

We noticed that when we presented animals occasional identical-object trials, they had perfect accuracy on probe trials with different objects. We decided to conduct a supplementary analysis on performance of probe trials over successive blocks of six trials collapsed over type of probe. We did this analysis to see whether there was a learning effect by rats in both groups. Figure 15 shows fixed and varied group performance for finding the target feeder on the first choice on different-object probe trials. As seen in the

figure, there is an increase in accuracy for locating the target feeder in both groups, $F_{2,20}$ = 21.88, p < 0.001, suggesting that the animals had learned how to successfully complete the task. Further analyses were carried out with paired samples t-tests examining changes in fixed group 1st choice performance over successive blocks of six probe trials, and found a significant increase on the second or third block from that of the first block, t_5s = 3.42, 9.03, ps < 0.01. The same analysis for the varied group found significant increases in performance on the second and third block of probe trials from that of the first block, t_5s = 2.23; 3.95, ps < 0.05; 0.01; and also a significant increase on the third block from that on the second block, t_5 = 2.24, p < 0.01.

Experiment 2B:

Figure 16 shows group differences on identical object probe trials. As the Figure shows, removing the differences among objects had no effect on the varied group's perfect accuracy for locating the 'correct' missing object-cued feeder under any of the probe test types. The fixed group also continued to accurately find the correct target feeder on the first choice when the test array was only moved from the location of the study array. However when the test array was rotated or when both rotated and moved, n this group's average number of choices to find the target feeder was virtually at chance. These observations were confirmed by significant interaction between probe type and group $F_{2,20}$ = 10.82, p < 0.01. Post-hoc t- tests between groups, found that the observed differences between groups on rotation and combination probes significant, t_{10}s = 16.07; 6.07, ps < 0.01.

Discussion:

We evaluated how successful two groups of rats were in finding a target object using relevant environmental cues. The fixed group received the same configuration, in the same location, and objects with the same relative position between trials; whereas the varied group received the same configuration, in a different location, and objects with a different relative position between trials. Both groups of rats received configuration rotations between trials. Both groups of rats were given probe trials wherein the configuration was either rotated in the test segment of the trial, relocated within the test segment of the trial, or both rotated and relocated within the test segment of the trial. We also presented rats with identical object probe trials wherein rats were presented with each type of probe trial variation, however all objects were identical in the test segment. We predicted that rats in the fixed group would reach criterion for completing the training phase significantly faster than rats in the varied group. We also predicted that rats in the varied group would complete all variations of probe trials with greater accuracy than rats in the fixed group. Moreover, we predicted that rats in the fixed group would experience greater disruption when presented with identical object probes than rats in the varied group.

The results obtained support our first prediction, that fixed group rats would acquire the training task earlier than varied rats. Although we were unable to run a statistical analysis on the acquisition data of the rats in the experiment discussed in Chapter 2, we found that fixed rats reached criterion before varied rats, therefore this prediction was supported by both experiments. Based on these results, and based on traditional theories of association proposed by Rescorla and Wagner (1972) and Pearce (1987,1994) it is reasonable to predict that rats presented with fixed information would

acquire the initial task earlier than rats presented with varied information. For rats in the fixed group, there was less information to separately process, that is various types of information could be processed simultaneously. For rats in the varied group, however, the environmental information changed from trial-to-trial, therefore giving the rats more variable information to encode, and this ultimately puts greater demand on the animal's visuo-spatial working memory.

We hypothesized that rats presented with fixed information would process cues simultaneously and that rats presented with varied information would process cues separately. We predicted that the animals in this experiment would engage in hierarchical search based on the results reported by previous literature (Arain et al., 2012; Arain & Cohen, in press; Brodbeck, 1994; Hodgson & Healy, 2005; LaDage et al., 2009). Given this hypothesis, we predicted that rats in the varied group would complete rotation probe trials with greater accuracy than rats in the fixed group. We based this prediction on results obtained from the Chapter 2 experiment, and on the results obtained by the Arain et al. (2012) study, which found that rats presented with varied information processed cues separately. The results obtained support this prediction. When a configuration was rotated within a trial, the correct global position was, at times, made irrelevant, as was the correct orientation. To successfully complete a rotation probe trial, the rat could only use the local object information, or the non-spatial featural object information. Our results also supported the prediction that rats in the varied group would complete the combination probe trials with greater accuracy than rats in the fixed group. When presenting the animals with combination probe trials, the correct orientation was made irrelevant, as was the correct global position. The animals could still use the

correct local position, as well as the correct non-spatial featural information to successfully complete these trials. We predicted that rats in the varied group would complete the location probe trial with greater accuracy than rats in the fixed group. We based this prediction on our previous research, which suggests that changing a cue that was initially fixed would disrupt the performance of an animal that has processed the environmental cues simultaneously. This prediction was not supported by our results: we found no significant group differences on location probe trials. In a location probe trial, the only piece of environmental information made irrelevant was the correct global position. Moreover, the animal could use the correct orientation, local position, or object information to complete this type of probe trial. Arain and Cohen (in press) presented rats with the same paradigm used in the present study. When giving the rats opposed-cues trials to assess hierarchical cue preference, they found that rats used non-spatial object featural information, before they used the local position, and then orientation and lastly the global position. According to these results, rats presented with the location probe trial should have no trouble successfully completing the trial, as rats rarely use the correct global position to complete this task. Therefore, when all other types of information are available to the animal, the animal can still complete the task with high accuracy, regardless of whether it has been previously presented with fixed or varied environmental information. We see something very different when two cues are made irrelevant. In rotation and combination probe trials, the relative orientation was rendered unusable, as was the global position. Even though Arain and Cohen found that on this task, rats use the orientation and global cues last, it still seems as though the animals are using the correct relative orientation in some way, as there were significant group differences.

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Moreover, from our results, it appears as though rendering two cues irrelevant significantly disrupts how a rat in the fixed group retrieves previously encoded information, but does not disrupt how a varied rat uses this information. These results support our hypothesis, that fixed rats processed environmental cues simultaneously, and varied rats processed environmental cues separately. However, it appears as though both groups were processing global position cues separately. Our results extend the findings of Arain et al. (2012) as we continued to show that rats presented with varied information experienced enhancement on probe trials, however in our preparation, rats presented with fixed information experienced disruption when given probes. Arain et al. only examined a varied group and were therefore unable to draw conclusions about how a fixed group would perform on probe trials. Our results also confirm results obtained in two studies using a 4-arm radial maze. In two separate studies, Cohen and Bussey (2005), and Tremblay and Cohen (2007) presented animals with fixed information in each radial-maze arm. Both studies revealed that rats presented with fixed information experienced significant disruption when presented with probe trials. In the present study, we were able to empirically test Arain et al.'s (2012), Cohen and Bussey's (2005), and Tremblay and Cohen's (2007) hypotheses and synthesize these findings into a single experiment.

We observed that in Experiment 2A, both groups' performance on probe trials significantly improved. This is interesting, as our initial findings support the notion that the fixed group was processing environmental stimuli simultaneously, and that the varied group was processing these cues separately. Although this was evident in initial probe trials, these group differences had disappeared after 18 probe trial presentations. These results suggest that rats in the fixed group began processing environmental stimuli

separately. These results further extend the idea of context-dependency (Herborn et al., 2011), as they support the notion that animals use different processing strategies, depending on the way that environmental information is presented, and dependent on the task at hand.

We presented the rats with identical object probe trials, wherein non-spatial object information was made unusable by the animal. We predicted that varied rats presented with rotations of the array of identical objects, changes in array location and combinations of these two within-trial changes would not disrupt their accuracy to find the missing objects, as they would the fixed rats. The results obtained support these predictions in terms of identical object rotation and combination probe trials, however did not support the prediction that varied rats would significantly outperform fixed rats on identical object location probe trials. In the Arain et al. (2012) study, rats presented with varied information between trials were successful on identical-object probe trials. Varied rats in this experiment also appeared to complete identical-object probe trials successfully. In this paradigm, Arain and Cohen (in press) found non-spatial object information to be the cue initially preferred by the animals, therefore it makes sense that animals that have been processing fixed information would experience disruption when these cues are made irrelevant. In identical object location probe trials, the non-spatial information as well as the global information is made irrelevant. Under these conditions, the performance of both groups of rats did not appear to be disrupted.

Our results imply that the orientation cue may be a more preferred cue than found in by Arain and Cohen (in press). In the present experiment, we added three distinct panels to the walls of the apparatus to give the animal a greater sense of absolute

direction. It could be that the animals in the Arain and Cohen's study were not provided

with strong directional-distal cues thus promoting their reliance on feeder orientation and

global position as their second-to last and their last choices in the opposed-cues trials.

These results support Jacobs and Schenk's (2003) contention regarding the importance of

directionality, as it is seen that when eliminating the use of orientation, animals

processing information simultaneously experience disruption. The present study extends

the previous findings of Arain, Parameswaran and Cohen (2012), as we found that

presenting rats with varied information produced separate processing. Moreover, we

added a fixed group and found that by presenting rats with fixed information,

simultaneous processing occurred. Our research also showed that with greater

experience, rats that initially showed simultaneous processing switched strategies and

began processing environmental stimuli separately. Therefore, our results also support

the notion of context-dependency proposed by Herborn, Alexander and Arnold (2011),

and provide a good example of differential processing on the same task.

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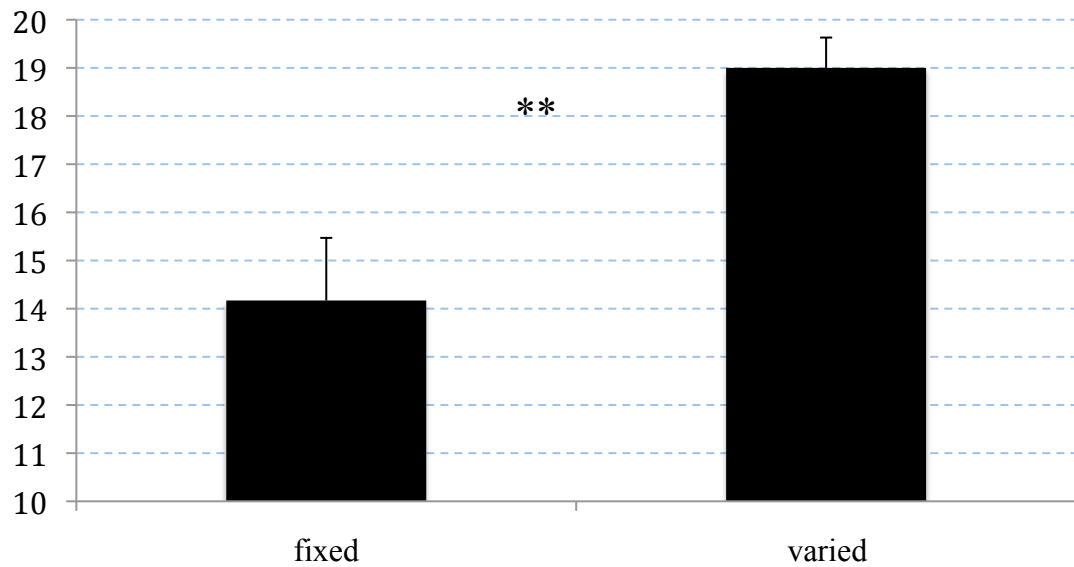
Number of Trials Until Criterion Reached

Figure 11: Acquisition data for Experiment 2. This graph depicts how many trials it took rats in the fixed group and the varied group to reach criterion for completing the training phase.

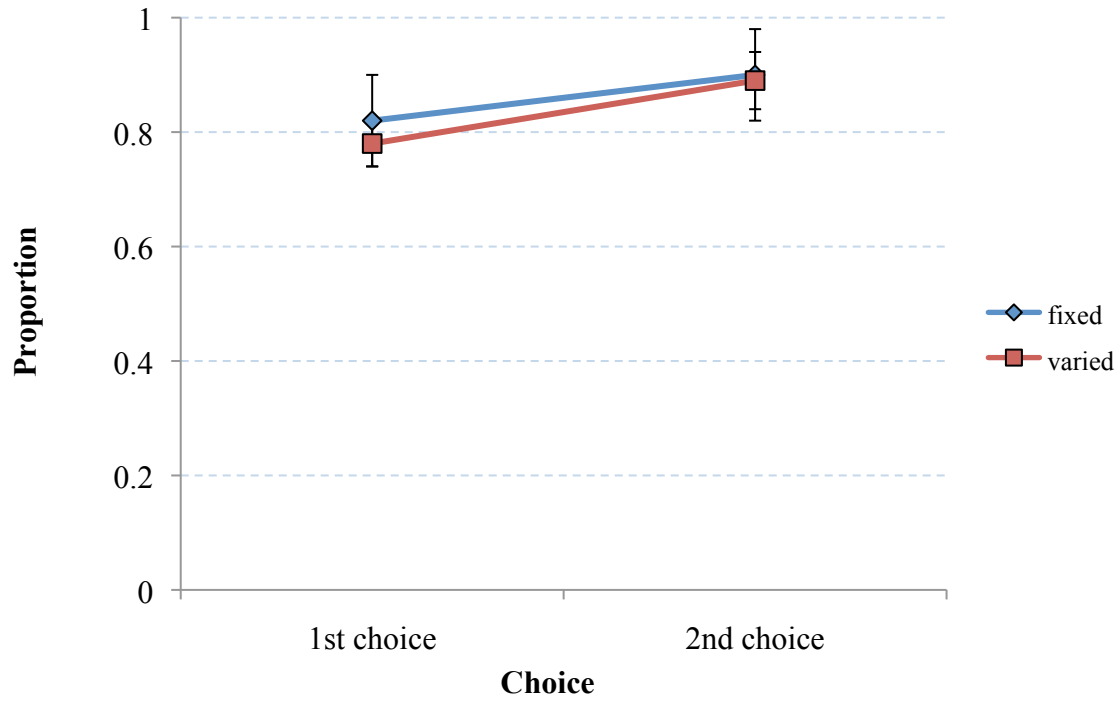**Proportion of Correct Choices on Acquisition Training Trials**

Figure 12: The proportion of trials the target feeder was selected by the 1st or 2nd choice on acquisition training trials for each group.
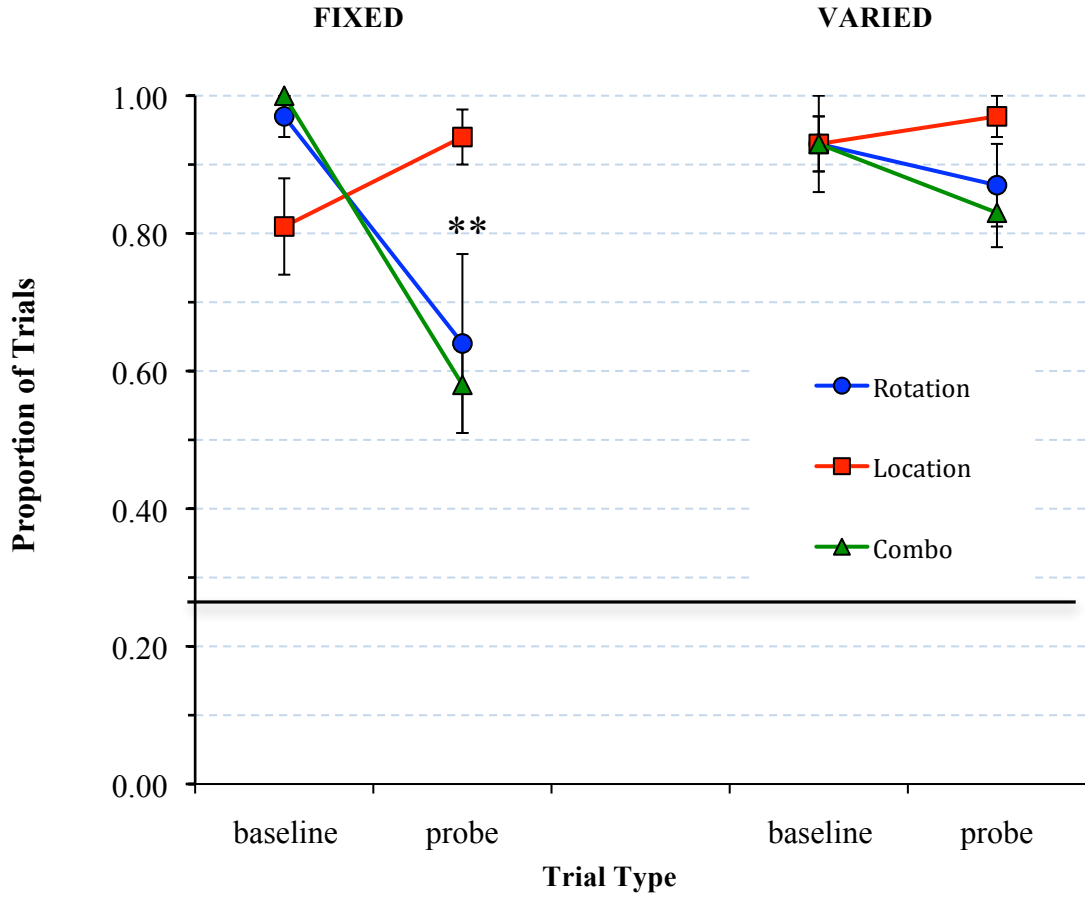
Target Object Found by 1st Choice

Figure 13: Rats' accuracy in finding the target feeder on different-object probe trials. Both fixed and varied groups' performance on all three types of probe trials are shown. The solid horizontal line represents the chance level.
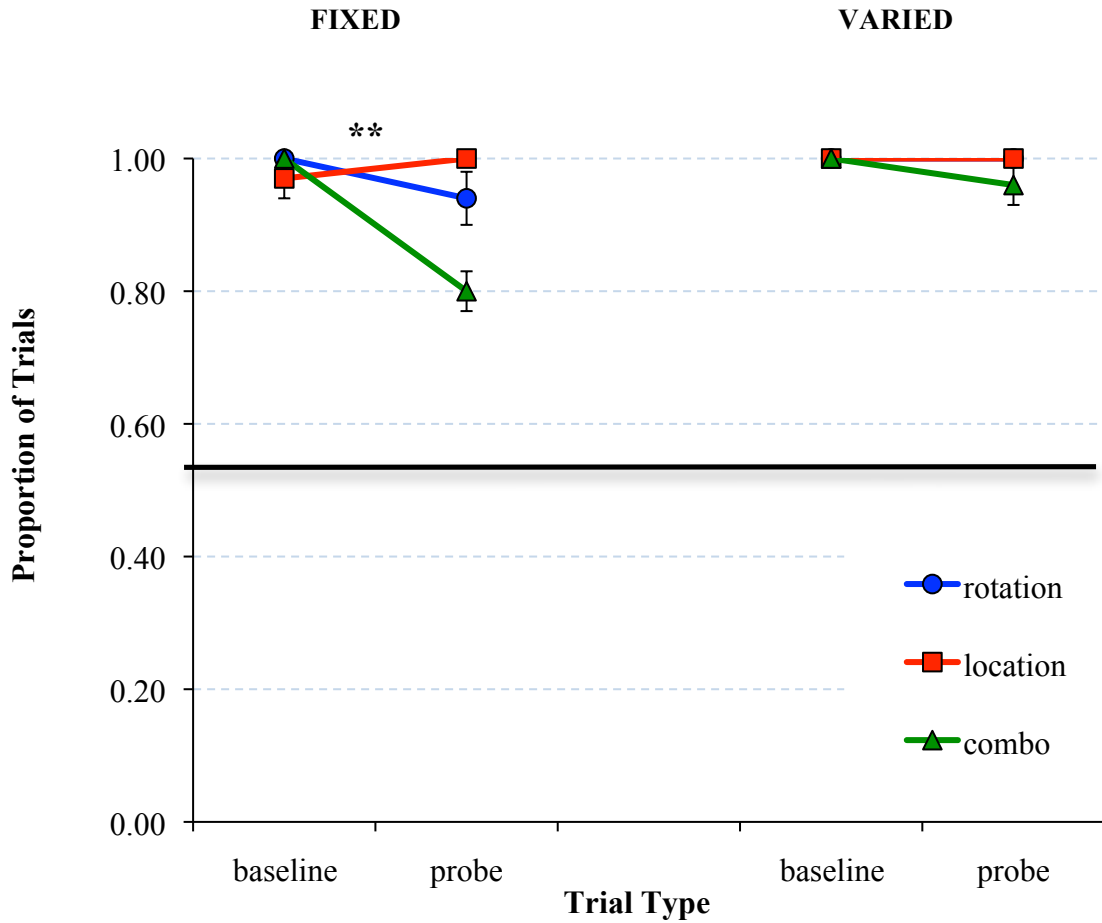
Target Object Found by 2nd Choice

Figure 14: Rats' accuracy in finding the target feeder by the second choice on different-object probe trials. Both fixed and varied groups' performance on all three types of probe trials are shown. The solid horizontal line represents chance.

Accuracy in Locating the Target Feeder on Different-Object Probe Trials
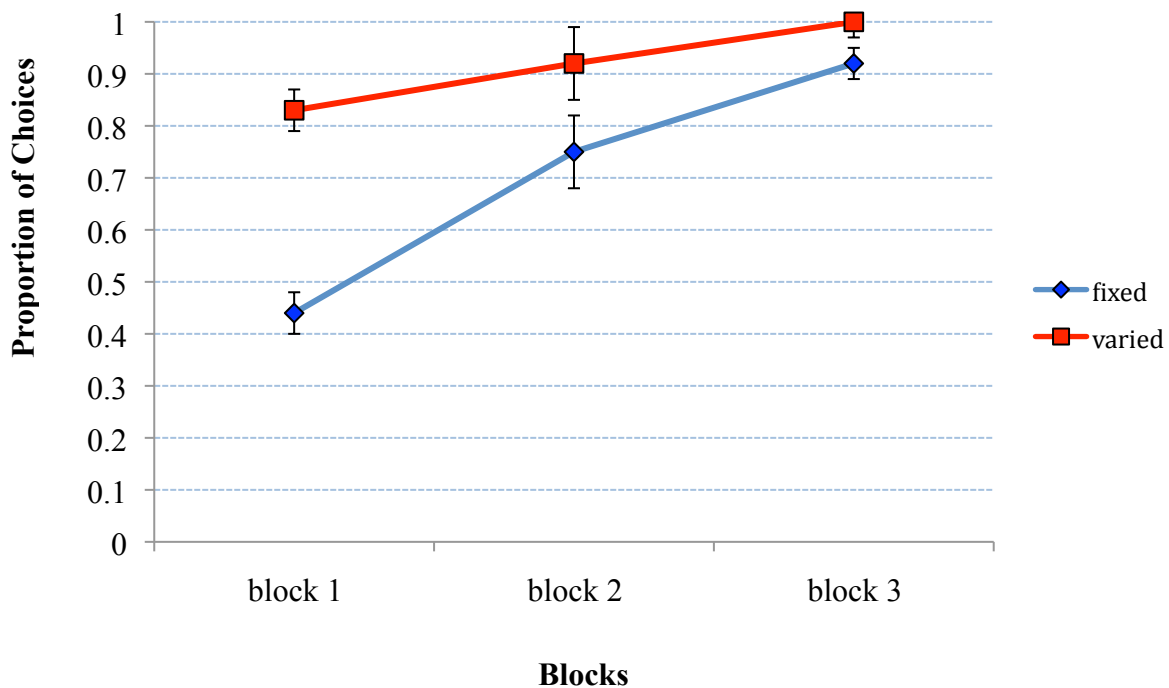

Figure 15: Rats' accuracy in finding the target feeder on different-object probe trials. Both fixed and varied groups' performance is broken down into three blocks of six trials.
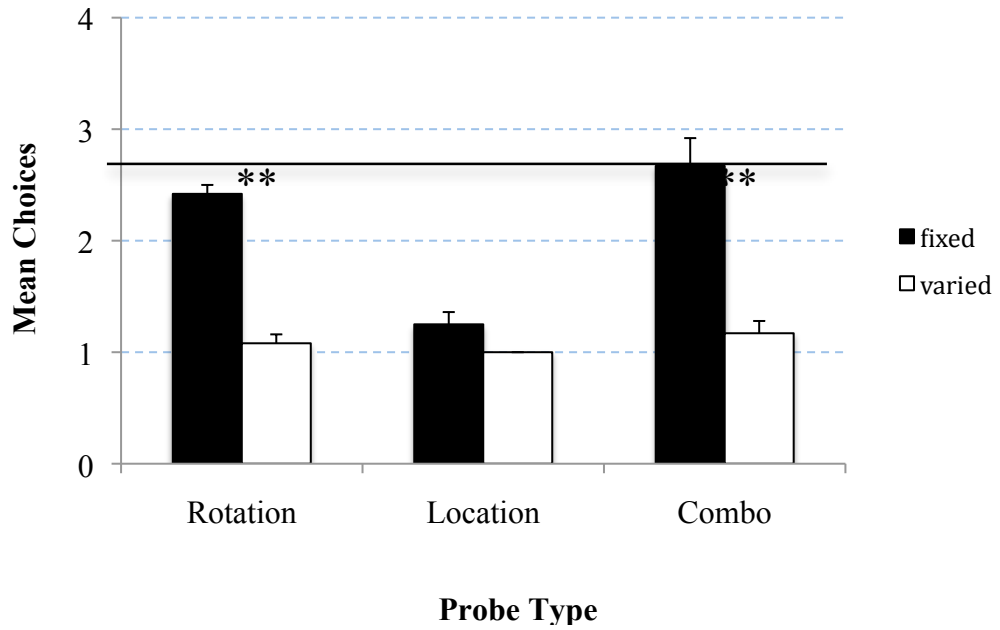
Identical-Object Probe Performance

Figure 16: Rats' accuracy in finding the target feeder on identical-object probe trials. Both fixed and varied groups' performance on all three types of probe trials are shown. The solid horizontal line represents chance

CHAPTER 4

GENERAL DISCUSSION

In the present experiment, it was found that the orientation cue is highly valuable to rats when completing a segmented-trial task. This was not found by Arain and Cohen (in press), however the orientation cue may not have been as pronounced in their experiment. Future research must present rats under both fixed and varied conditions with opposed-cues probe trials to reassess the hierarchy of cues. Moreover, it is highly important that the absolute orientation is established by giving the animal some type of distinct cue to differentiate between directions, such as the panels used in the present experiment. Baddeley and Hitch (1974) proposed that animals mentally represent environmental information in working memory for a limited period of time, until they have completed the task that requires this information. The length of time that information can be stored in working memory and then later used is important, when studying visuo-spatial working memory. Arain, Parameswaran and Cohen (2012) presented rats (*Rattus norvegicus*) with segmented trials with varying ISIs: Rats were either given a 2-minute ISI between trial segments, or they were given a 30-minute ISI between trials segments. Future research should implement different ISIs to determine how long this information can be held in working memory and whether this will affect its later use.

As is common in animal experiments, we used solely male subjects in our experiments. One of the reasons why female animals are underused in animal research is their estrous cycle (Westwood, 2008). Moreover, the animal's estrous cycle can potentially produce disruption in the animal's regular activity, and this can ultimately

hinder the results obtained from the experiment (Westwood, 2008). Although there

appears to be greater challenges in terms of working with female animals, it is important

that females are added to the experimental sample, as significant sex effects have been

found: It has been found that male and female animals process environmental

information differently, and use these types of information differently when foraging

(Barkely & Jacobs, 2007; Bettis & Jacobs, 2012; Chai & Jacobs, 2010; Costanzo, Bennett

& Ludermann, 2009; Smulders, Gold & Lever, 2010). For instance, Langley (1994)

found that female desert kangaroo rats (*Dipodomys deserti*) used the shape of the arena

and the location of objects to locate a goal, whereas males solely used geometric cues. It

has also been observed in various studies that females use non-spatial details of local

landmarks, whereas males rely more on geometric and distal information when

navigating (Galea & Kimura, Gibbs & Wilson, 1999; MacFadden et al., 2003; Sandstrom

et al., 1998). Given these findings, future research should examine sex effects by

presenting this task to both male and female animals, as well as presenting opposed-cues

trials to both sexes to determine how the two sexes process information and whether they

process this environmental information differentially and whether this can be influenced

by the way in which information is presented to the animal.

Our research provides evidence of a paradigm wherein two groups of animals of

the same species were found to process environmental information differentially,

depending upon the cues available and the stability of the cues presented. Our research

also provides evidence of changing processing strategies depending on the task. Previous

research has focused on hoarding behaviour as a predictor of how animals process and

utilize environmental information (Barkley & Jacobs, 2007; Batty et al., 2009; Brodbeck,

1994; Hodgson & Healy, 2005; Hurly et al., 2010; LaDage et al., 2009; Macdonald, 1997; Watanabe, 2005). Recent research, however, places greater emphasis on the actual task at hand, or the context in which the information is presented (Herborn, Alexander & Arnold, 2011) and this helps explain the mixed findings found in research using hoarding behaviour to predict foraging behaviour. Different species were considered to have specialized memory systems based on hoarding behaviour, however our research suggests that the context can override species-specific characteristics. Furthermore, our research builds a bridge between the general-process view and the species-specific view by suggesting that the general laws of learning can ultimately be determined by considering species-specific behaviours and how these behaviours can be controlled to prevent them from interfering with general processes. Our research is significant in that it builds upon the notion of context-dependency and it introduces the idea that different processing strategies are used depending on the information available. This is especially important when assessing which strategies are used by animals when foraging, as certain environmental cues remain static in an environment, whereas others are subject to frequent change. Given these circumstances, our research suggests that visuo-spatial working memory processing is dependent on the stability of cues in the environment, and this provides us with a greater understanding of how animals use various types of environmental information to forage efficiently.

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VITA AUCTORIS

NAME: Corrine Keshen

PLACE OF BIRTH: Toronto, ON

YEAR OF BIRTH: 1989

EDUCATION: Westmount Collegiate Institute, Thornhill, ON, 2007

The University of Western Ontario, B.A., London, ON, 2011

University of Windsor, M.Sc., Windsor, ON, 2013