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Information Seeking in Rats on the Radial Maze

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Graduate Program in Psychology
A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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INFORMATION SEEKING IN RATS ON THE RADIAL MAZE

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by

Chelsea R. Kirk

Graduate Program in Psychology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

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Abstract

Metacognition is awareness of what one does and does not know. Students given a choice between studying material they have learned well and material they have learned poorly prefer to study the less mastered material (Metcalfe, 2009). Recent studies suggest that primates also know about the state of their own knowledge and will seek unknown information to complete a task (Call & Carpenter, 2001; Hampton et al., 2004). Two experimental paradigms can be used to test for the presence of metacognition within a species: uncertainty tasks and information seeking tasks. Uncertainty tasks ask animals to judge their confidence in the information that they possess. Information-seeking studies ask animals to recognize that they have insufficient information to complete a task and then study their response to such a situation. To form a strong argument for the presence of metacognition within a species, both metacognition tasks should be investigated. I used a radial arm maze to look for information-seeking behaviour in rats. Each maze arm had a bulb mounted on it to serve as a signal light. Rats were trained to go to whichever arm was lit on a trial for reward. They then were trained to press a bar in the maze hub that led to immediate food reward and turned on a light in one randomly chosen arm of the maze. Once the rats learned to press the bar, the reward for bar pressing was discontinued. I report on the rats' readiness to press the bar for information about the location of reward under conditions that varied the presence or absence information and amount of information to be gained.

Keywords: Rats, information seeking, metacognition, comparative cognition

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Information Seeking in Rats on the Radial Maze

Metacognition can be described as an awareness of what one knows and what one does not know; it is the ability to access the contents of one's own mind (Roberts, McMillan, Musolino, & Cole, 2012). Specifically, metacognition allows an individual to determine if a specific item of information is present within memory. The critical feature of this cognitive capacity is an awareness of the presence or absence of the information in question, meaning that subjects have a subjective sense of "knowing" and "not knowing" and can distinguish between these two knowledge states. Furthermore, metacognition posits that the ability to take an internal inventory of the information available to an individual should also be used to alter future behaviours, making this phenomenon tractable to scientific study.

Metacognition is commonly used by students when taking a test. Employing this cognitive faculty means that a student has a subjective awareness of the presence or absence of information needed to answer a specific question on the exam. The knowledge state regarding the accessibility of the necessary information is available to the student without requiring him/her to actually produce the answer to the question. The student is not required to consciously search through memory to become aware that the information is accessible. Students are also able to use these knowledge states to alter their future behaviour, such as determining which material to study and when to terminate review of specific facts. This behavioural outcome provides a quantifiable measure of metacognition within this population. In fact, students given a choice between studying material they have learned well and other material they have learned poorly show a strong preference for study of the less well mastered material (Metcalfe, 2009).

What species are capable of using metacogniton? Researchers have been examining this question in a variety of species for the past 15-20 years, beginning with dolphins (Smith et al., 1995) and igniting a flurry of experimental studies and review papers on the topic in the last 10 years (e.g., Kornell, 2009; Smith, Beran, Couchman, & Coutinho, 2008). A substantive body of comparative literature has emerged that, coupled with research on human metacognition, allows psychologists to begin hypothesizing about the evolutionary pressures which selected for such a cognitive capacity.

Paradigms for Examining Metacognition

Historically, two experimental paradigms have been used to test for the presence of metacognition: the uncertainty task and the information seeking task. The first task is used when a subject gives a confidence rating on the accuracy of a behaviour, such as performing a difficult perceptual judgement or completing a memory test for information studied earlier. Confidence can be measured pre-test or post-test. For example, a pre-test judgement would require the subject to decide whether to perform a perceptual discrimination or escape the trial before actually performing the discrimination; this decision is based on how certain the subject is that it can perform the future discrimination accurately. In a post-test judgement, the subject would first complete the perceptual discrimination and then report either a high or low level of confidence in the accuracy of that past response. When experimenters use uncertainty paradigms, they are interested in a subject's awareness that a memory may have degraded over a delay interval or that increasing difficulty in a perceptual discrimination could result in an inaccurate judgement. Nelson and Narens (1990) termed this general process as "monitoring" of information by the individual.

Comparative psychologists have tested this ability through use of the uncertainty task. For example, Smith et al. (1995) began a trial by presenting a bottlenose dolphin (*Tursiops truncates*) with a tone ranging from 1200 Hz to 2100 Hz. The dolphin then classified this tone as either “High” or “Low”. Initial discrimination training sampled stimuli on the outer ends of the frequency range, producing relatively easy trials for learning. Once the subject had acquired the task, intermediate frequencies were introduced to increase the difficulty of the task. The subject was trained to respond to three response paddles, one indicating that it heard a high sound (located on the left side of the testing tank), a second indicating that it heard a low sound (located on the right side of the testing tank), and a third representing an “escape” response. A correct response resulted in food reinforcement and praise from a trainer. An incorrect response produced a 9-s time-out. Responses to the escape paddle aborted the current trial and caused an easy trial (1200 Hz, classified as “low”) to begin. This escape option allowed the animal to abstain from making a difficult perceptual discrimination by bringing on an easy trial; however, the dolphin experienced a slight delay to reinforcement by choosing the uncertainty response due to the increased swimming distance to the paddle and the need to wait through another trial to correctly answer the easy discrimination. Thus, using the escape response resulted in an outcome of intermediate value between correct and incorrect responses. Results showed dolphins performed in a manner similar to that of humans tested on an analogous task, with use of the escape response highest when the task was most perceptually difficult. The dolphins also showed an increase in behaviours that are characteristic of human uncertainty, such as an increased latency to respond as task difficulty increased.

Smith et al. (1995) designed a paradigm that asked the subject to make a perceptual judgment about a stimulus. Correct judgments were rewarded with food reinforcement and incorrect judgments resulted in an aversive timeout. However, the critical aspect of this design was the third response option which allowed the subject to escape difficult trials. Results showed that at frequencies close to the animal's discrimination limit, the subject chose to forgo guessing if the frequency was high or low, instead choosing the escape response and accepting a short delay in exchange for the presentation of an easy discrimination trial. This behaviour suggests that the subject was aware that it could use the escape response when it was uncertain. Finally, the dolphin's behaviour mapped very closely onto that of human subjects tested on a similar paradigm, providing further evidence that the same inner mental state was experienced by the animal as by the human subjects.

With respect to the second metacognition paradigm, comparative psychologists are interested in what animals do when information that they require is absent from memory. While the uncertainty task examines animal behaviour when judgment is difficult based on available information, it is also possible that a subject could have no information at all that is relevant to the task. The subject would need to be aware of this deficiency in order to seek out further information when appropriate. The second paradigm then investigates information-seeking behaviour. Information-seeking studies present the animal with a procedure for which it does not possess enough information to complete. The animal's behaviour is then monitored to see if it subsequently seeks out further information from the environment to help it complete the task. Metacognition is investigated by asking if the animal is aware that it does not hold enough information in memory to complete a task. An animal's behaviour is examined to see if it attempts to seek information necessary to make a correct response. Nelson and Narens (1990) described this effect of knowledge state on behaviour as "control".

Hampton, Zivin, and Murray (2004) performed an exemplary study on information-seeking in rhesus monkeys (*Macaca mulatta*). Nine subjects were presented with four opaque tubes, one of which was correct for each trial. Monkeys were allowed to make one choice, with the purpose being to choose the tube which contained a high-value food reward. Pulling on a tube indicated a choice; if the choice was incorrect an intertrial interval began without reward, but if the choice was correct, the reward would slide out of the tube and into the monkey's reach. Experimenters manipulated the presence or absence of information available to the monkeys through two different trial types: seen and unseen. On seen trials, subjects were permitted to watch the experimenter bait the tube before being allowed to make a choice. On unseen trials, an opaque screen was placed between the subject and the experimenter during the baiting procedure. After baiting was complete, the opaque screen was lifted and monkeys were then allowed to choose a tube. The design of this study suggests that monkeys should know where food is located on the seen trials and should not know where food is hidden when the baiting procedure was occluded on the unseen trials. Results showed that, on seen trials, monkeys simply reached for the tube where they had witnessed the experimenter placing a reward. However, when the baiting procedure was hidden from view on the unseen trials, subjects produced an interesting behaviour: they bent down and looked through the tubes to see which of the four options held the reward. After doing a visual search to obtain information about the location of the reward, monkeys would then reach out and choose the correct tube. Almost all subjects performed this looking behaviour significantly more often when they had no information about the task than when they had seen the baiting procedure. Looking behaviours represented an attempt to seek out more information about a task when subjects did not know the location of the food reward on a trial. The results suggest that the monkeys were able to subjectively judge whether or not they had the required information to complete the task. The difference between their looking behaviour on the seen and unseen trials suggests that the monkeys were able to use the state of their own knowledge to decide whether or not to look for information.

Hampton et al. (2004) provides a comprehensive example of information-seeking research in non-human animals. Subjects were only allotted one choice per trial, and therefore it was very important that monkeys gained as much information about the task as possible before performing a choice. However, because bending down to look through tubes in search of food takes time and creates an inherent delay to reinforcement, looking behaviour should only be performed when it is necessary to the animal. The findings suggest that monkeys were sensitive to their own mental states. On seen trials, when subjects knew the location of food, they rarely spent time performing a visual search for food and instead immediately made a choice. This behaviour is in comparison to unseen trials, when the subjects lacked information about where the reward was hidden and attempted to seek out information about the task before responding. The results indicate that subjects had control over their own information-seeking behaviour but only used it when appropriate to maximize reward. Subjects were not simply looking down all tubes at all times, but were systematically deciding when it was necessary to look and when they possessed enough information to answer immediately. These findings with rhesus monkeys are very similar to those found with 2.5-year-old humans (Call & Carpenter, 2001), showing that such an effect has been found in both human and non-human primates.

In general, information-seeking studies are designed so that on some trials an animal has sufficient information to complete the task, while on other trials they begin with insufficient information. Subjects are monitored for how they respond on these insufficient trials. One possibility is that the subject could guess which alternative is correct for that trial. In the Hampton et al. (2004) study, monkeys could have guessed by simply choosing one of the four tubes at random during the unseen trials. The other, more interesting, alternative is for the animal to begin seeking out more information from the environment that is relevant to the task. If animals seek out information only when appropriate (only on these uninformed trials), then it suggests that they have access to the contents of their own memories and are aware of when they lack information.

To summarize, there are two experimental approaches for testing for the presence of metacognition in animals. Uncertainty tasks ask animals to judge their confidence in the information that they possess. Information-seeking studies ask animals to recognize that they have insufficient information to complete a task and then study their response to such a situation. To form a strong argument for the presence of metacognition within a species, both metacognition tasks should be investigated.

Metacognition Across Species

A comprehensive review of the literature should take into account both of the experimental procedures previously discussed. In addition to a focus on the paradigm of a study, attention should also be paid to the species used in a particular study. The literature review will begin with research done with human subjects to establish a benchmark for comparison, as humans are a species which can give verbal reports of the subjective experience that accompanies the employment of metacognition. Studies involving non-human species will then be discussed to develop a truly comparative understanding of metacognition as a cognitive faculty within the animal kingdom.

Humans. Metacognition has been examined extensively in humans (*Homo sapiens*) and theories about the underlying processes of human metacognition often serve as the starting point for experimental questions in comparative studies. The use of metacognition by humans seems to be so second-nature that human subjects rarely require any training on such tasks in the laboratory (Kornell, 2009). The subjective awareness that individuals experience has been referred to as "monitoring", while the observable effect of this process on the behaviour that the subject performs (such as choosing to terminate studying) is termed "control" (Nelson & Narens, 1990). These dimensions of metacognition are investigated using the uncertainty paradigms and information-seeking paradigms, respectively.

What benefit does metacognition provide to the individual? Metcalfe (2009) argues that the implementation of metacognition allows humans to effectively take control of their own future learning. Subjects who are able to make accurate judgments of their own knowledge states and then capitalize on those judgments to alter future behaviour are able to successfully increase their proficiency with the material at hand (Metcalfe, 2009). The ability to appropriately seek information allows for more efficient allocation of both mental and physical resources.

What exactly are subjects describing when they report an inner state of uncertainty? Schwartz, Benjamin, and Bjork (1997) posit that human subjects use internal cues to infer the strength (and thereby presence) of knowledge in memory. This inferential process is dependent on a variety of other information sources to arrive at a judgment of certainty. For example, an individual could use a strong feeling of familiarity associated with the memory item in question to determine that knowledge is present in memory. Some scientists have raised concerns over the reliability of human self-reports as indicators of inner mental states. Nelson (1996) proposed that scientists use self-report data as an additional information source: introspective reports can be analyzed like other forms of behavioural data and thereby corroborate experimental findings. In this way, self-reports of internal mental states can be studied in the same fashion as other observable behaviours.

A wealth of experimental data on human metacognitive behaviour exists, and many of these findings are presented in comparison to behaviour from non-human species. When asked to monitor the contents of their own memories, human subjects reliably chose to take memory tests when that information (correct answers) was readily available in memory, and refused to take memory tests when the information was degraded due to a retention interval or a challenging serial position location (Smith, Shields, Allendoerfer, & Washburn, 1998). Smith, Shields, Schull, and Washburn (1997) found that humans consistently chose to escape from experimental trials that presented a difficult perceptual discrimination. Using a second perceptual judgment task, Smith et al. (1997) also found individual differences between human participants with respect to their escape behaviour, which mirrored individual variability seen in non-human primate findings. Humans have been shown to use metacognitive strategies adaptively in a variety of paradigms (Smith, Shields, & Washburn, 2003), suggesting that the ability can be applied in novel ways. Information-seeking behaviours are also used flexibly; adults choose to study material of varying difficulty depending on the amount of study time allowed, focusing on more difficult information as study time increases (Son & Metcalfe, 2000). The human behaviours outlined here have been used as a benchmark for comparative work, as can be seen in the similarity between animal and human paradigms.

It is worth noting that humans do not always perform in a way that is most efficient or most appropriate with regard to metacognitive behaviour. In their review of student study habits, Kornell and Bjork (2007) emphasize that proper information-seeking habits are not entirely innate and that students can be taught to improve their approach to studying. The variability in human behaviour also becomes apparent when algorithms are used to model optimal performance on a task, such as that done by Smith et al. (1995). Results from their human participants mapped fairly well onto the most optimal simulation; however, it was clear that humans were not completely maximizing reward through their introspective judgments.

Developmental literature. Developmental psychologists have shown an interest in the extent to which children are capable of making metacognitive judgments. Many studies focus on three- or four-year-old children due to the fact that they are able to make verbal responses in regard to their inner mental states. Findings suggest that children have some metacognitive ability at age four, but are lacking various aspects of the fully developed ability they will have as adults. For example, O'Sullivan (1993) found that four-year-olds knew that more time spent studying an object led to better retention when given a memory test, a finding that is consistent with data from adult subjects. However, Miscione, Marvin, O'Brien, and Greenberg (1978) demonstrated that four-year-old children struggle to differentiate between internal states such as "forgetting" or "knowing", mental conditions which are an integral part of the adult metacognitive experience. Additional studies have shown that elementary school children can judge their own internal knowledge states but struggle to implement this information into changes in behaviour (Schneider & Lockl, 2002).

Children performed better when tested using paradigms which did not require verbal responses. Call and Carpenter (2001) found that 2.5-year-old children performed information-seeking behaviours appropriately when asked to choose the location of a hidden reward. Children performed visual searches when the baiting procedure had been hidden from them, but refrained from searching when they had seen the baiting take place.

A review by Schneider and Lockl (2002) reported that the developmental literature suggests that children improve on a variety of metacognitive tasks as they progress through development. Most studies they considered showed that children's performance is similar to that of adults by age eleven or twelve, presumably because of the large amount of metacognitive training that young children receive in school, such as being asked how well they remember concepts previously covered in class (Kornell, 2009). Comparative psychologists will find this developmental framework largely informative as they extend theories regarding the presence or absence of metacognition in non-human animals.

Non-Human Primates. Many studies in recent years have examined the metacognitive-like abilities of a range of non-human primate species. The work previously mentioned by Call and Carpenter (2001) examined the information-seeking behaviours of chimpanzees, orangutans, and 2.5-year-old children, concluding that all subjects showed an efficient employment of information-seeking behaviours without requiring training by the experimenters. Rhesus macaque monkeys performed similarly when tested using an analogous task (Hampton et al., 2004). Rhesus macaques and human subjects have also been found to perform similarly when tested using same-different judgments. Both species were found to escape from difficult trials which required the subject to make a difficult discrimination response near their psychophysical threshold (Shields, Smith, & Washburn, 1997). Rhesus macaques have also been shown to rapidly adapt their uncertainty responding to novel tasks without additional training (Washburn, Smith, & Shields, 2006). Orangutans (*Pongo pygmaeus*) perform efficient visual searches to determine the location of food and have been documented to infer the location of a reward if all other locations have been examined (Marsh & MacDonald, 2012a). Work by Suda-King (2008) also suggests that at least some orangutans have knowledge about when they lack information needed to complete a task. Thus, experimental reports suggest that chimpanzees (*Pan troglodytes*), orangutans, and rhesus macaque monkeys share many of the features of metacognition possessed by humans.

Although the metacognitive abilities of the above species have been shown to be comparable, studies done with capuchin monkeys (*Cebus apella*) demonstrate that they fail to perform at a similar level. Basile, Hampton, Suomi, and Murray (2009) examined memory awareness in capuchin monkeys and found that subjects were not able to employ the same information-seeking approach that the other species used to complete a visual search task. Monkeys often performed more looking behaviours than were necessary and looks down tubes were not shown to increase accuracy on a trial, suggesting that subjects were not actually gathering information by looking. Paukner, Anderson, and Fujita (2006) used an analogous looking-task and again found problems with the pattern of looking behaviour performed by capuchins. Subjects often performed unnecessary looks down transparent tubes and looked down bent tubes which provided no visual information regarding the presence or absence of food, findings consistent with Basile et al. (2009). Using a paradigm developed for pigeons, Beran and Smith (2011) found that both rhesus macaques and capuchin monkeys would respond to see a stimulus if they needed the identity of the stimulus to complete a test. Further experimental manipulations showed that macaques were able to flexibly transfer this ability to novel trial types, while capuchins failed to do so, making errors similar to those made by pigeons (Roberts et al., 2009). Fujita (2009) found support for a more basic form of memory awareness in capuchin monkeys. One monkey was found to reject memory tests when it had not been shown a sample, suggesting that it was aware that it lacked the information necessary to complete the test. However, another experiment with the same subject found no difference in performance between tests that it chose to take and tests that it was forced to take, suggesting it was not differentiating between knowing and not knowing during testing. In total, these results imply that capuchin monkeys may not possess a form of memory awareness found in humans, chimpanzees, orangutans, and rhesus macaque monkeys.

Other species. Comparative psychologists have begun to expand their investigations to non-primate species. Comparing across multiple species allows for the discussion of phylogenetic origins of metacognition. Smith et al.'s (1995) work with the bottlenose dolphin was an early expansion into metacognition work in non-primate mammals. Results showed that the subject reliably escaped from discriminations when stimuli were at its psychophysical limit. Data from this dolphin mapped onto data from human subjects completing an analogous task.

Many studies have investigated the presence of metacognition in birds, with an emphasis on pigeons. Adams and Santi (2011) found that pigeons (*Columba livia*) produced higher accuracy on memory tests that they chose to take as compared to forced memory tests. However, this effect was only found after the birds had received extensive training. Inman and Shettleworth (1999) also reported mediocre performance in pigeons on a metamemory task. In their studies, birds appropriately used a safe key to escape from a memory test when difficulty increased with the addition of a delay interval. Pigeons were also found to have higher accuracy on chosen memory tests than on those they were forced to take. However, this was only true if the escape key was presented concurrently with the response alternatives; birds were not able to use the escape key if it was presented before the response options for that trial. Sole, Shettleworth, and Bennett (2003) also found that pigeons responded appropriately on trials in which they experienced a high level of uncertainty; however, unlike the Inman and Shettleworth (1999) findings, these birds were no better on chosen tests than on forced tests, and therefore the overall findings are inconclusive. Sutton and Shettleworth (2008) also examined metacognition in pigeons using the uncertainty paradigm. They failed to find evidence that pigeons could use an escape response appropriately before completing a visual discrimination. Subjects also failed to employ confidence ratings concerning their accuracy on discriminations that they had previously completed.

A comprehensive set of studies by Roberts et al. (2009) failed to find evidence that pigeons possess metacognitive capabilities. Pigeons were tested on a delayed matching-to-sample paradigm. Pigeons were allowed to choose between two alternatives: one presented the sample stimulus required to complete the matching-to-sample test, and the other omitted the sample stimulus and progressed directly to the comparison stimuli. Results indicated that that pigeons preferred the alternative that progressed directly to the comparison stimuli without presentation of the sample stimulus. Subjects did not respond to see the sample stimulus which provided information that could then be used to perform the visual discrimination at a high level of accuracy. In a following procedure, pigeons were presented with a sample stimulus for .5 or 5 s. Allowing the pigeons to observe the sample stimulus for .5 s produced a weak memory of the stimulus identity, and a strong memory was produced when the pigeons viewed the sample stimulus for 5 s. Pigeons were then allowed to choose between the two alternatives from the previous experiment: one alternative presented the sample stimulus (with this second presentation now serving as a reminder of the sample identity) while the other alternative immediately presented the comparison stimuli. The experimenters hypothesized that pigeons would respond to the alternative with the reminder of the sample when they had a weak memory trace due to the original .5 s presentation of the sample. They also predicted that the birds would respond to the alternative that immediately presented the comparison stimuli when they had a strong memory of the sample identity due to the original 5 s sample presentation. Results indicated that birds rarely responded for this reminder of the sample regardless of the strength of their memory trace. Birds strongly preferred to move directly to the comparison stimuli. In a final experiment, delay to reinforcement was equated. Pigeons first performed a peck to the centre key to initiate a trial. Subjects were then presented with two comparison stimuli, coloured red and green, with red appearing on the left key on 50% of trials and on the right key on 50% of trials. A white centre key was also present and could be pecked once to present the sample that matched one of the comparison stimuli. Pigeons could respond to the centre stimulus and then use its identity to perform a simultaneous match-to-sample discrimination, or they could forgo the sample stimulus and respond to the comparison stimuli without the information concerning which identity was correct for that trial. Roberts et al. (2009) found mixed results. Some birds behaved in a manner consistent with metacognition by pecking the centre stimulus to view the sample before choosing a comparison stimulus. Some birds performed in a non-metacognitive manner by always choosing a comparison stimulus without viewing the sample identity. The data from the remainder of the birds were inconclusive, with only a portion of responses made to view the sample stimulus. Zentall and Stagner (2010) responded to these studies by designing a similar paradigm which equated for delay to reinforcement for informative and non-informative alternatives. They found that, when the differential delay between the two alternatives was removed, pigeons responded to the informative alternative. These findings suggest that pigeons may choose informative over non-informative alternatives, but only when the effort required in doing so is minimal.

Other bird species have also been studied: work with large-billed crows (*Corvus macrorhynchos*) found that crows were not able to use an escape response appropriately to avoid difficult trials, but that subjects were able to provide accurate confidence ratings on memory tests that they had already taken (Goto & Watanabe, 2012). The authors concluded that large-billed crows may possess retrospective metamemory but are unable to perform prospective judgments based on memory contents. In another study, bantams (*Gallus domesticus*) and pigeons were tested for their ability to rate their confidence in the accuracy of perceptual discriminations they had performed. Both bantams and pigeons were able to rate their confidence in the accuracy of their own responses post responding for a trial (Nakamura, Watanabe, Betsuyaku, & Fujita, 2011).

In summary, numerous studies have shown that birds fail to use an escape response appropriately to cancel trials in which uncertainty is high. Birds also fail to respond to informative stimuli (compared to uninformative stimuli) unless many precautions are taken to ensure that the delay to reinforcement associated with the informative side is minimal. Overall, it appears that birds do not possess metacognitive capabilities equal to those of primates.

Limited research has been completed by experimenters interested in canine metacognition. McMahon, Macpherson, and Roberts (2010) tested dogs (*Canus familiaris*) in a series of experiments on metacognition. They found that dogs would not reorient themselves in space in order to collect visual information required to complete a discrimination task, suggesting that dogs are not able to accurately perform information-seeking behaviours like those found in primates. Brauer, Call, and Tomasello (2004) also failed to find evidence for information seeking in dogs when dogs had the opportunity to view the location of food reward before choosing between two boxes. However, further manipulations by McMahon et al. (2010) found that dogs chose a human with information about a food finding task (who would point to the location of food) over a human with no information about the task (who stood with her back to the dog). Similar to findings with birds, the canine research suggests that dogs may have a more rudimentary form of metacognition than primates, although more work remains to be done with this species.

Finally, Foote and Crystal (2007) investigated metacognition in the rat (*Rattus norvegicus*) using a duration-discrimination paradigm. Rats had to classify tones lasting for 2 and 8 s as short or long. Rats were then tested with intermediate tone lengths, so that the discrimination grew difficult at durations near 4 s. On some trials, rats were given the option of declining to take the test after hearing the sample tone (escape response), and on the remainder of trials the rats had to complete the discrimination. Rats were found to reject tests at the most difficult intermediate tone lengths, indicating that they were aware of their own uncertainty concerning the correct classification of the tone. Results also showed that rats performed significantly better on the most difficult trials when they had chosen to take the test as opposed to when they were forced to take the test, a finding that has been considered critical evidence for primate metacognition. In summary, the work done by Foote and Crystal (2007) provided preliminary evidence that rats may possess metacognitive-like abilities.

Evolution and Metacognition

The presence of metacognitive-like capacities in multiple species suggests that evolutionary pressures may have favoured animals which were able to monitor their own memories. It is not difficult to imagine that the ability to identify information that an individual lacks could be beneficial for future decision-making. Additionally, an awareness of how certain or uncertain an animal is concerning its own decision-making can improve outcomes for that individual.

To better understand how metacognition evolved, it is critical that a variety of species is studied. The literature suggests that, in general, mammals have experienced the strongest selection pressure for this cognitive faculty, especially primates. In contrast, birds show much weaker evidence of metacognition; therefore, environment demands on birds may not have required such rigorous examination of an individual's mental states.

Current Hypotheses

The four studies presented here investigate several aspects of metacognition in the rat. The questions addressed will be in keeping with those asked in the past of human and nonhuman subjects. Experiment 1 asked if rats would perform an information-seeking behaviour (lever press) to receive information necessary to complete a task. Rats were initially directly reinforced for pressing a lever that provided a light cue directing them to the arm of an eight-arm radial maze containing an additional reward. After rats learned to press the lever and go to the correct cued arm, direct reinforcement for lever pressing was discontinued. It was hypothesized that rats would continue to press the lever in order to obtain a signal light indicating the location of food. An alternative outcome predicts that rats would extinguish lever pressing and search for the food reward at random without information.

In Experiment 2, the information afforded by the signal light was made no longer necessary to complete the current trial by providing rats with a reference memory that indicated the correct arm. It was hypothesized that rats would now extinguish lever pressing behaviour because the information provided by the lever press was redundant with reference memory information. An alternative account suggests that rats would continue to press the lever to turn on the light for conditioned reinforcement, showing that they had not pressed the lever for information provided by the signal light.

In Experiments 3 and 4, the rats' sensitivity to the amount of information provided by the signal light was tested. Trials containing different amounts of information were presented to the rats. It was hypothesized that rats would be more likely to press the lever as the amount of information gained for a lever press increased. Rats with metacognition should be sensitive to the amount of information obtained from the signal light and should alter their behaviour accordingly. Marsh and MacDonald (2012b) presented orangutans with a similar procedure, and orangutans increased their information-seeking behaviour as the amount of information to be obtained increased. The fact that the orangutans' behaviour tracked the changes in the task implies that the orangutans recognized the amount of information to be gained and altered their behaviour based on that knowledge state.

Experiment 1

In Experiment 1, I examined whether rats would perform an information-seeking behaviour in order to acquire information about the location of a hidden food reward. Similar to work done by Foote and Crystal (2007), the behavioural measure was trained by the experimenter. Rats were trained to press a lever for food reinforcement, with the lever placed in the centre of an eight-arm radial maze. For each trial, rats were also required to find the correct arm (randomly chosen) out of eight possible arms where food was hidden. Of critical importance, pressing the lever both delivered an immediate food reward (in the form of a sugar pellet) and provided information needed to find the arm containing food (communicated through a signal light denoting the correct arm). During the testing phase of Experiment 1, the immediate food reward was discontinued and rats received only information about the location of the correct arm when they made a lever press response. I was interested in whether rats would continue to lever press for information or would instead extinguish lever pressing and begin searching the eight arms randomly to complete the trial. Experiment 1 served as the foundation for the current program of study, as it is reasonable to expect a rat to prefer information to its absence if that animal possesses metacognitive-like abilities.

Methods

Animals. Subjects were ten adult male Long-Evans hooded rats (*Rattus norvegicus*). Rats were roughly 100 days old and experimentally naïve when they began Experiment 1 training. While participating in training and testing, subjects were maintained at approximately 85% of their free-feeding weight and were always allowed access to water. They were housed individually in transparent plastic cages in a colony room maintained at 22 degrees Celsius. Colony room lights were illuminated at 7 a.m. and extinguished at 7 p.m. All testing took place between 10 a.m. and 5 p.m. five days per week.

Apparatus. A wooden eight-arm radial maze served as the apparatus (see Figure 1). The maze consisted of a centre hub with arms extending outward from the centre. The diameter of the entire maze measured 196 cm and the diameter of the hub measured 36 cm. The apparatus was placed on stabilizing posts which secured it 61 cm above the floor. The hub of the maze was painted white. Each arm was 80 cm long x 9 cm wide and was painted black. All arms were spaced equally apart from one another. A light grey plastic food cup with a diameter of 5 cm was attached to the distal end of each arm, and a white signal light with a diameter of .5 cm was mounted vertically 5 cm above the end of the arm. The height of the light ensured that the light was level with the rat's head. A control panel allowed the experimenter to set the light on any arm to come on when the lever was pressed. Located in the center of the hub was a black plastic food cup measuring 4.5 cm in diameter. Research Diets 45 mg sucrose pellets were delivered through a tube into this food cup by an electromechanical pellet dispenser mounted above the maze. Also in the centre of the hub was a metal lever which rats were trained to press. The lever was 1.5 cm long x 1.5 cm wide and extended from a metal box that measured 8.5 cm long x 5.5 cm wide. The pellet dispenser, the signal lights, and the response lever were controlled electronically by a box outside of the maze, measuring 26 cm long x 22 cm wide x 8 cm tall. A white noise generator emitted background noise to mask possible distracting sounds. All training and testing took place in a semi-darkened room measuring 27 m long x 38 m wide x 24.5 m high.

Procedure.

Habituation. Before beginning the experiment, rats were handled daily by the experimenter. To habituate the rats to the maze, they were allowed to explore the hub and arms of the maze. During this time, rats were allowed to eat reward pellets on the

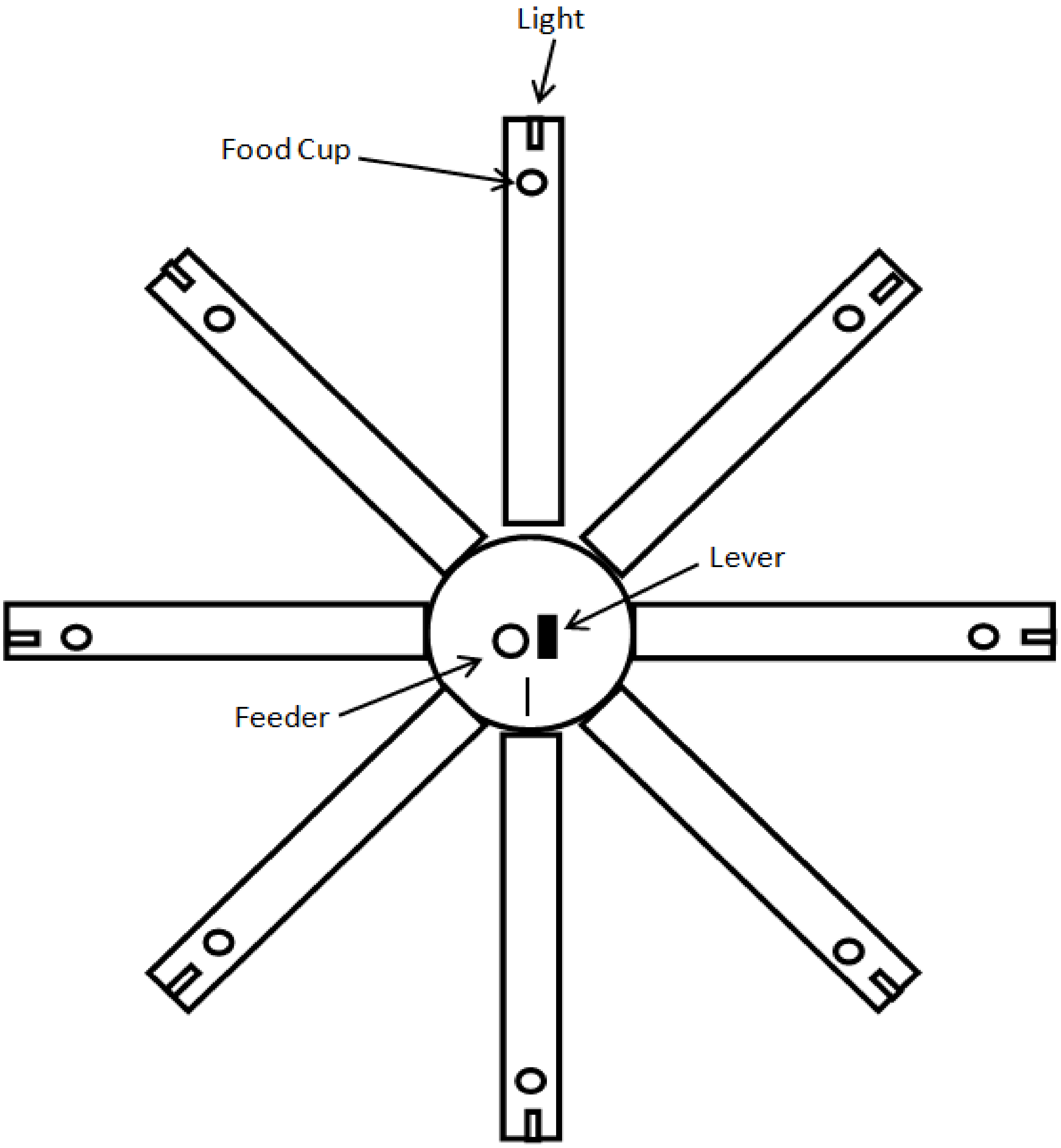

Figure 1: Visual representation of the radial arm maze, as seen from above.

maze and were exposed to the sound of white noise. The habituation phase lasted 15 days.

Light Pre-Training. During this phase of pre-training, rats learned that an illuminated signal light on the distal end of an arm indicated three 45 mg sucrose pellets were hidden in that arm's food cup on that trial. Each day, a rat received one trial of training in which it was placed in the hub of the maze and one of the signal lights on one of the arms was illuminated. The rat was allowed to freely investigate arms of the maze until it had entered the correct arm and consumed the food reward. Light pre-training continued until all rats were reliably approaching the correct arm on their first or second search. Light pre-training lasted 30 days.

Lever Press Pre-Training. After the completion of light pre-training, rats were shaped using operant conditioning to perform lever presses. Successful responses were reinforced automatically by the pellet dispenser. Training times varied among rats, but all lever press pre-training was completed in three weeks.

Experimental Training. Rats then began the final phase of training. They were given one trial per day in which one of the eight arms was randomly chosen to be correct. The food cup on this arm was baited with three reward pellets. When a trial began, rats were placed in the hub of the maze. Rats were allowed to freely search all eight of the arms to seek out the correct arm. A lever press immediately resulted in two things: a pellet reward was delivered to the food cup in the hub of the maze and, simultaneously, the signal light on the correct arm was illuminated. Critically, rats received both an immediate food reward and information about the correct arm by completing a lever press. The trial was terminated when the rat selected the correct arm and consumed the contents of its food cup. All searches made by a rat were recorded. The training phase of Experiment 1 continued until rats were pressing the lever at a high rate (on over 90% of trials) and were reliably choosing the correct arm on their first or second search. This phase of training lasted about four weeks.

Testing. Rats were then placed on experimental testing. Each rat received three trials per day for 15 days of testing. For each trial, one of the eight arms was pseudo-randomly chosen to be correct so that all eight arms were correct an equal number of times. As in training, the food cup on the correct arm was baited with three pellets. At the start of each trial, rats were released into the hub of the maze and allowed to search for the correct arm. If the rat pressed the lever during testing, the signal light on the correct arm would be illuminated; however, no pellet reward was delivered to the food cup in the hub of the maze. It is critical to note that during testing, rats received only information about the current arm location of reward when they completed a lever press and were no longer immediately reinforced for this behaviour. The trial ended when the rat selected the correct arm, regardless of whether it had pressed the lever or not, and all searches made by the rat were recorded. Rats reached asymptotic behaviour after 15 sessions, and testing lasted three weeks.

Results

Experimental data showed variability with regard to when rats chose to press the lever during a trial. On some trials, rats would press the lever before making any searches. On other trials, rats would complete some number of searches before performing a lever press. On the remainder of the trials, rats did not press the lever before the trial ended. In an attempt to account for this variability, data were coded in two ways. One coding system, called Press First, only scored a trial as containing a lever press if that lever press was performed before any searches were executed by the rat. The second coding system, called Press Ever, scored all trials as lever press trials when a lever press was performed at any time during the trial. These two coding systems present a strict interpretation of the information-seeking behaviour by selecting all non-initial presses (Press First) and a more relaxed interpretation (Press Ever), which allows for investigation of rats' overall lever-pressing behaviour.

Graphical displays of the probability that a trial contained a lever press during Experiment 1 can be found in Figure 2. All curves were created by averaging three trials per rat for all 10 rats each session. Figure 2 shows the acquisition and testing curves for the Press First dataset, in which trials were coded as containing a lever press only if that press occurred before any searches to the maze arms were performed. At the start of training, rats were pressing the lever before performing any searches to maze arms at a low level (on approximately 30% of trials). During this phase, rats received an immediate reward in the hub for pressing the lever. As a result of this reinforcement, rats became more likely to press the lever before performing any searches. At the conclusion of training, rats were pressing the lever in this manner on approximately 95% of trials. Rats were then transitioned to the testing phase in which the immediate food reward for lever pressing was withheld so that rats received only information about the location of hidden food. Initially, the probability that rats would press the lever dropped to about 65% on session six of testing but quickly recovered to approximately 85% of trials at the conclusion of testing. Figure 2 also shows the acquisition and testing curves for the Press

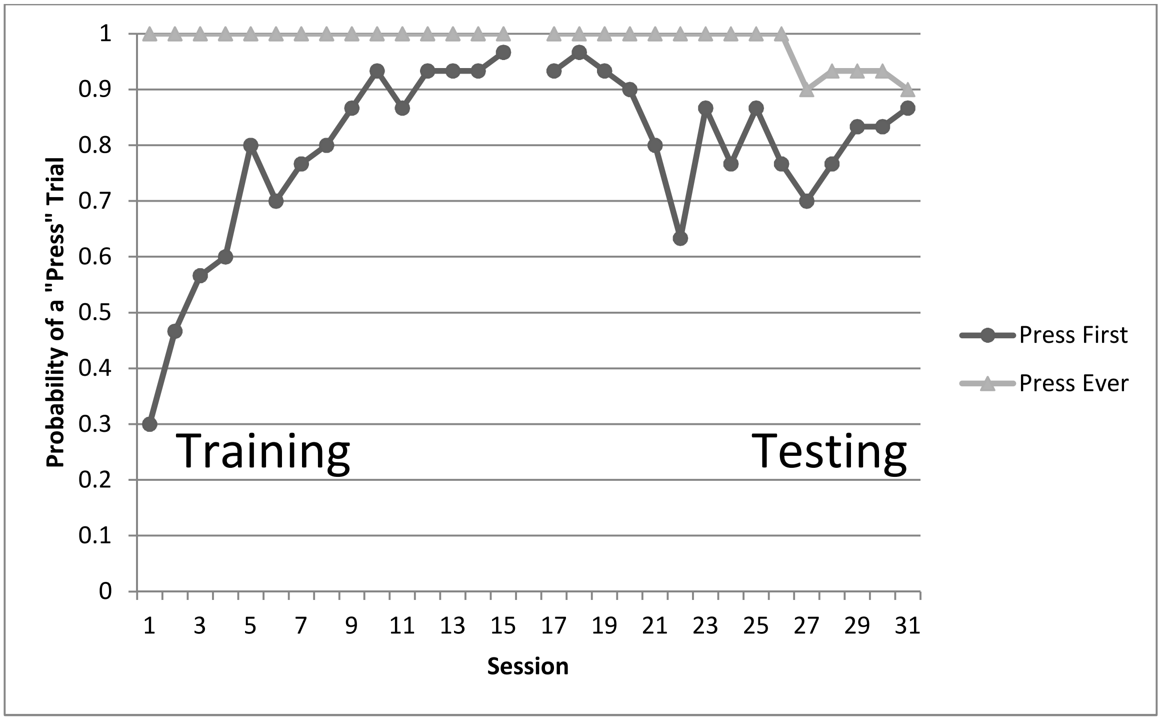

Figure 2: Graphical presentation of the lever pressing behaviour for the Press First (closed circles) and Press Ever (closed triangles) datasets in Experiment 1.

Ever dataset. The Press Ever dataset represents all trials in which a lever press occurred at any time before the completion of the trial. During training, all rats performed a lever press at some point during the trial for all trials; they received the immediate food reinforcement for performing this behaviour. During testing (when the immediate food reinforcement was not delivered), rats continued to press the lever at a high rate. Rats were pressing the lever before performing searches to the maze arms on 90% of trials at the completion of Experiment 1 testing.

A repeated-measures analysis of variance was performed on the Press First dataset to assess the acquisition of the lever pressing behaviour during the training phase of Experiment 1. Results indicated that rats significantly increased their lever pressing during training, $F(14, 126) = 8.8$, $p < .001$. The significant change within the data suggests that the likelihood that rats would press the lever before performing any searches on a trial increased significantly as rats progressed through training. With respect to the Press Ever dataset, all rats pressed the lever at some point in all trials during the training phase. Statistical analyses were not performed on these data due to the lack of variability within the dataset. When examined in concert, the Press First and Press Ever datasets suggest that the rats altered their lever pressing behaviour from occurring at any point during a trial to occurring immediately at the beginning of the trial during this training phase.

During the testing phase of Experiment 1, rats received information in the form of a signal light concerning the location of food when they performed a lever press. A repeated-measures analysis of variance was performed on both the Press First and Press Ever datasets to assess the effect of session on the likelihood that rats would press the lever. The results of the Press First dataset found no significant effect of session on the amount of lever pressing that was performed, $F(14, 126) = 1.62, p = .18$. Similarly, no significant effect of session was found in the Press Ever dataset, $F(14, 126) = 1.66, p = .21$. The two non-significant results indicate that, regardless of coding method, rats continued to press the lever to receive information about the task even though they no longer received an immediate food reward for doing so.

In order to directly compare the lever pressing behaviour observed in training and testing, a repeated-measures analysis of variance was performed, examining whether the likelihood that the rats would press the lever during last five sessions of training differed from the likelihood that they would press during the last five sessions of testing. Results for the Press First data set found that the lever pressing behaviour in the last five sessions of training and testing differed significantly, $F(1, 9) = 5.51, p = .044$. The observed difference between these stages suggests that rats were pressing significantly less often in the testing phase. The same analysis was performed on the Press Ever dataset. The lever pressing observed in training and testing was not found to be significantly different for this coding method, $F(1, 9) = 4.36, p = .066$. The lack of a difference between these stages indicates that rats did not change their lever pressing behaviour when they were no longer immediately reinforced for pressing the lever.

Figure 3 presents the rats' searching behaviour from the training and testing phases of Experiment 1. At the start of training, rats required slightly more than 6 searches per trial to find the arm with the hidden food reward. The accuracy of searching performed by the rats improved as they progressed through training, and rats completed training requiring slightly more than 1 search per trial to find the hidden food (near-

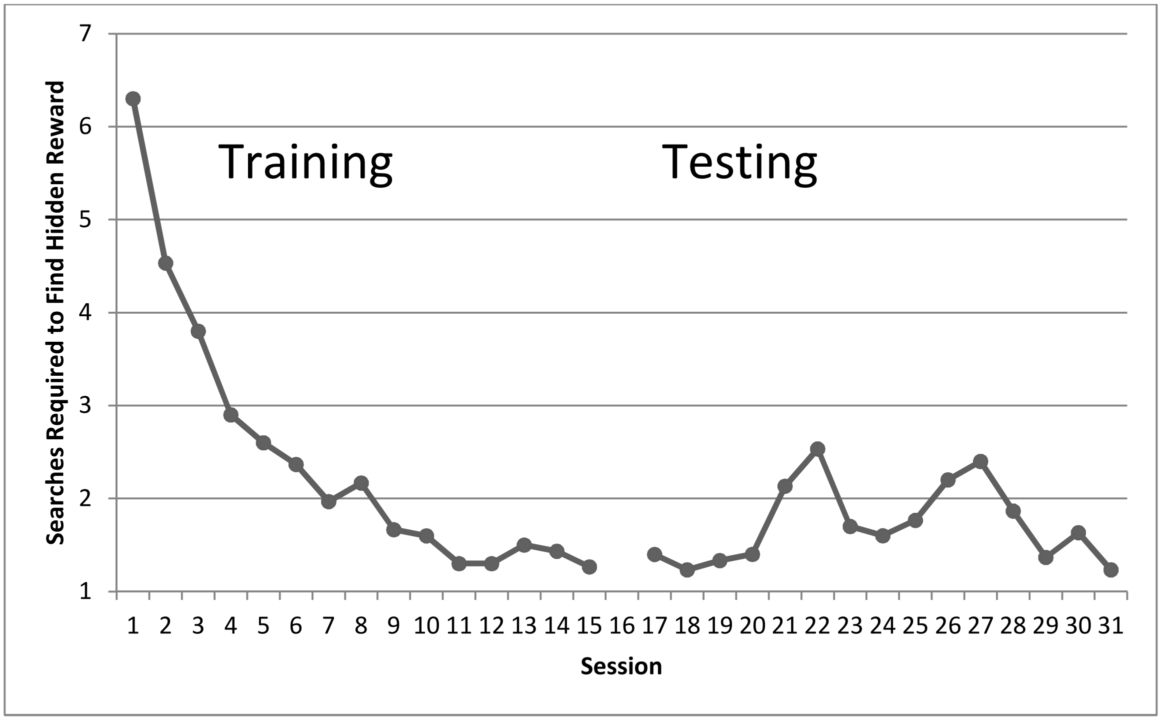

Figure 3: Graphical presentation of arm searching behaviour for Experiment 1.

perfect performance). During the testing phase of Experiment 1, rats continued to search efficiently, never requiring more than 2.5 searches per trial.

To examine the search behaviour of the rats in the training phase of Experiment 1, a repeated-measures analysis of variance was used. Across the 15 sessions of training, rats significantly decreased the number of searches they completed before finding the hidden food reward, $F(14, 126) = 8.28$, $p = .004$. The significant decrease in the number of searches indicates that rats significantly improved their searching accuracy as a result of the training. A repeated-measures analysis of variance was then performed to test the rats' search behaviour in the testing phase of Experiment 1. Results found that the number of searches that the rats completed before finding the hidden food reward did not significantly change during the testing phase, $F(14, 126) = 2.13$, $p = .10$. These results signify that rats maintained their searching proficiency throughout the duration of the testing phase; their search performance was not disrupted when the immediate food reward was withheld. Testing trials were then divided into those that contained a lever press and those that did not to compare the average number of searches required by rats to find the hidden food in these two types of trials. Cases of missing data (for example, if a rat pressed the lever on all trials during testing and therefore gave no value for searches without a lever press) were replaced using mean substitution to avoid removing the subject from the analysis. Mean substitution can inflate the likelihood of committing a Type 1 error and therefore conclusions should be interpreted with caution. A paired-sample t-test was used to compare the average number of searches required by rats to find the hidden food in trials in which they had pressed the lever compared to trials in which they had not pressed the lever. The analysis found that rats required significantly less searches to find the food when they had performed a lever press (*M* = 1.62, *SD* = .35) than when they had not pressed the lever (*M* = 5.4, *SD* = 2.14), $t(9) = -6.27$, $p < .001$. These findings suggest that rats employed information provided by the signal light to improve their searching efficiency.

Discussion

During the training phase of Experiment 1, rats received both an immediate food reinforcement and information concerning the location of hidden food when they performed a lever press. At the conclusion of training, rats were performing the lever-press behaviour at a very high rate. Analysis showed that rats significantly increased their lever pressing (according to the Press First coding procedure) during the training phase of Experiment 1. I was interested in whether rats were pressing the lever just to gain the immediate food reward or if they understood the value of the information afforded by the signal light. To test this, I removed the immediate food reinforcement. It was expected that rats would show continuous extinction of lever pressing if only the immediate food reward had supported the lever press. During testing, rats received only information about the task when they pressed the lever. A repeated-measures analysis of variance directly compared how likely rats were to press the lever during the training and testing phases of Experiment 1. Results found that rats significantly decreased their lever pressing when the data were coded using the Press First dataset, suggesting that the immediate food reinforcement played a role in supporting the rats' lever pressing behaviour. However, the rats were still pressing the lever on 87% of trials, and therefore rats continued to perform information-seeking behaviours on a large proportion of the trials. The high level of lever pressing performed at the end of testing was more clearly presented when coded using the Press Ever dataset. Results of the analysis of that dataset found that the rats did not significantly change their lever pressing behaviour between the training and testing phases. When these two datasets are examined in concert, they provide evidence that rats did not significantly decrease their lever pressing behaviour in response to the absence of the immediate food reward. The stability of the rats' lever pressing behaviour suggests that rats continued to perform this behaviour in order to receive information about the correct arm location. In total, these results suggest that rats will perform an information-seeking behaviour in order to gain information about the location of hidden food.

With respect to searching behaviour, rats required approximately six searches to arms of the maze before finding the correct arm when they began the training phase of Experiment 1. Over the 15 sessions of training, there was a significant decrease in the number of searches that rats performed before they chose the correct arm. The rats improved so much that they were showing almost perfect search behaviour at the conclusion of the training, requiring (on average) just over one search per trial. Rats maintained this high level of searching accuracy throughout the testing phase of Experiment 1, as the searching behaviour observed during this phase did not significantly change. A comparison of the number of searches required on trials with a lever press to searches required on trials without a lever press showed that rats searched significantly more accurately on trials in which they pressed the lever. The searching performance in Experiment 1 provides evidence that rats were able to use the information collected from the signal light to enhance their efficiency in finding the hidden food reward.

Experiment 2

The purpose of Experiment 2 was to determine if rats would stop performing an information-seeking behaviour (i.e., lever pressing) if they no longer needed the information provided by that behaviour to find the food location. In Experiment 1, rats could not predict the location of food from trial to trial, and therefore they relied on the information provided by a signal light to determine where food was hidden. In Experiment 2, food was always hidden on the same arm in Phase 1; thus, after some experience, rats should learn where food is located. Rats received no training for this experiment and were transitioned directly from the Experiment 1 procedure to that of Experiment 2. With experience, rats should come to know the location of food before ever entering the maze. This paradigm renders the signal light redundant, as a rat should not need to see the signal light to know where the reward is hidden. It was hypothesized that as rats formed a spatial memory for the location of food, they would begin to inhibit their lever-pressing responses. A subject with metacognition would be able to determine if specific information (i.e., the location of a reward) is present in memory, and therefore should not need further information (light cue) to complete the task. To strengthen our understanding of how flexible the rats' behaviour is in response to changes in the value of information provided by the signal lights, the contingencies were reversed in Phase 2 and the location of food was once again made unpredictable. It was hypothesized that rats would recover their lever-pressing behaviour in Phase 2 when the information provided by doing so was once again useful to them.

Methods

Animals and Apparatus. The animals and apparatus from Experiment 1 were used in Experiment 2.

Procedure. During this experiment, rats experienced a same-arm Phase 1 and a random-arm Phase 2. Experiment 2 testing began immediately after the completion of Experiment 1. For each rat, one of the eight maze arms was randomly chosen to always be correct (e.g., Rat 1 always found food on Arm 3 and Rat 2 always found food on Arm 8). The correct arm was baited with three pellets on every trial. A trial began when the rat was placed in the hub. If the lever was pressed, no pellet was delivered in the hub of the maze and the signal light on the correct arm of the maze was illuminated. Trials were terminated when the rat chose the correct arm. Rats received three trials per day for 30 days in Phase 1. The reversal procedure (Phase 2) was then performed; during this phase, rats were returned to the testing procedure from Experiment 1. That is, the correct arm changed randomly from trial to trial. Phase 2 required 20 days to complete.

Results

Data from Experiment 2 were coded in the same manner as in Experiment 1 so that two datasets were produced, one for the strict “Press First” coding procedure, and another for the more lenient “Press Any” coding procedure. Both datasets were analyzed in the same manner to obtain the following results.

The lever pressing behaviour that was observed during Phase 1 of Experiment 2 is graphically displayed in Figure 4. Figure 4 shows the data as coded using the “Press First” coding procedure. At the beginning of this phase, rats pressed the lever before

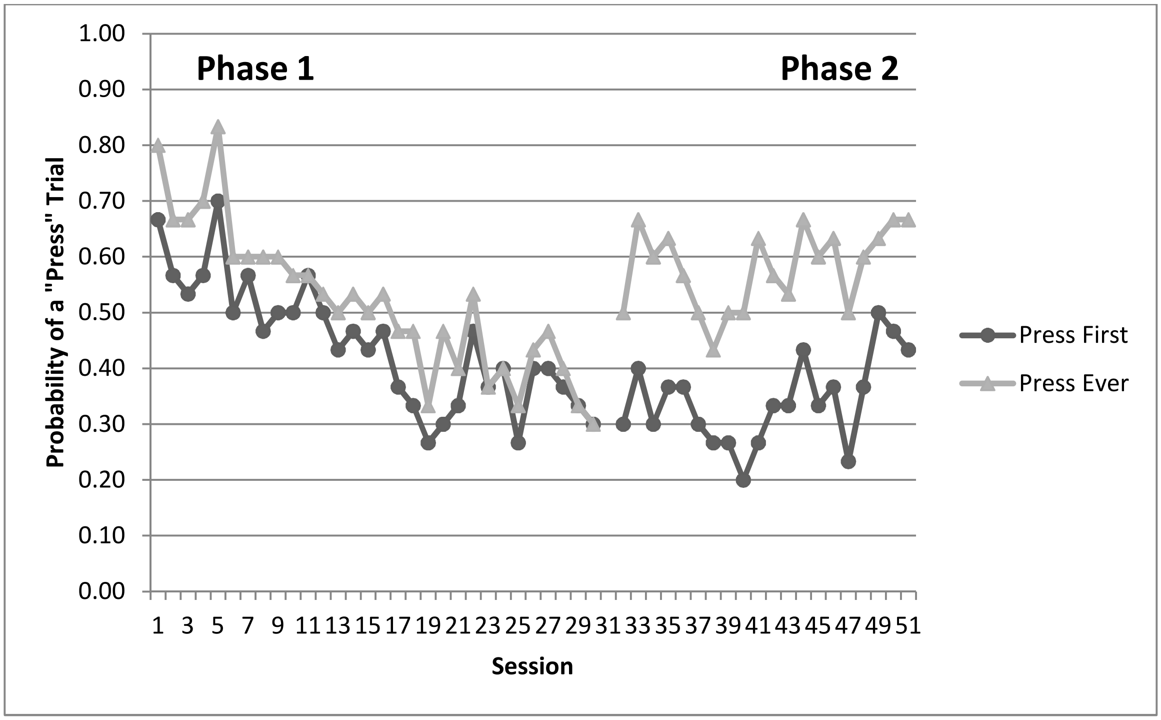

Figure 4: Graphical presentation of the lever pressing behaviour for the Press First (closed circles) and Press Ever (closed triangles) datasets in Experiment 2, Phases 1 and 2.

completing any searches on the majority of trials (approximately 67% of trials). During the 30 sessions of Phase 1 rats reduced the number of trials in which they pressed the lever before completing any searches, reaching 30% of trials at the conclusion of the phase. Figure 4 also presents the same data, but coded using the “Press Ever” coding procedure. At the beginning of Phase 1, rats were making a lever press response at some point during the trial on 80% of trials. This value decreased over the 30 sessions of testing; at the end of Phase 1, rats were pressing the lever at some point during the trial on 30% of trials.

In this experiment, rats first encountered a procedural change which rendered the signal light as redundant (Phase 1). To test if this change affected the rats’ likelihood of lever pressing to receive information about the location of food, a repeated-measures analysis of variance was performed. When using the Press First coding method, session significantly affected the rats’ probability of pressing the lever, $F(29, 261) = 2.77$, $p = .03$. Similarly, a significant effect of session was also found with the Press Ever coding method, $F(29, 261) = 4.27$, $p = .005$. These results show that rats significantly decreased their lever pressing when the signal light offered no additional information about the task.

A graphical representation of the searching behaviour observed during Phase 1 of Experiment 2 can be found in Figure 5. Rats began this experiment requiring slightly less than two searches per trial to find the hidden food reward, indicating that rats continued to search efficiently. Rats maintained good searching behaviour throughout the duration of Phase 1. By the conclusion of Phase 1, rats had returned to near-perfect searching accuracy and required slightly more than one search per trial (on average) to find the hidden reward.

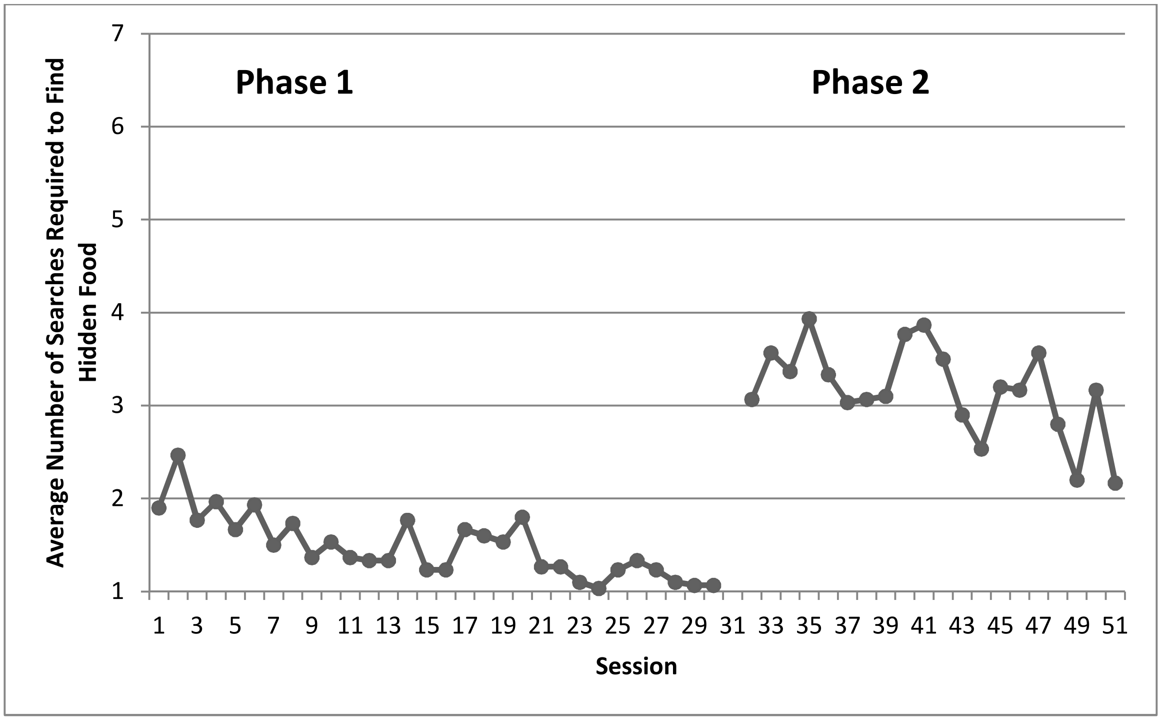

Figure 5: Graphical presentation of searching behaviour for Experiment 2, Phases 1 and 2.

To test for changes in the searching behaviour observed from the rats during this phase, a repeated-measures analysis of variance was conducted on the searching behaviour from Phase 1. Results found no significant effect of session on the number of trials that rats required to find the hidden food reward, $F(29, 261) = 2.6$, $p = .054$. These findings suggest that rats maintained a high level of searching efficiency without disruptions during Phase 1. Trials for Phase 1 were then divide into those that contained a lever press and those that did not to study how lever pressing affected searching proficiency in this phase. Mean substitution was used to replace missing data points to prevent the removal of subjects from the analysis. Results found no significant difference in the number of searches required to find the hidden food when rats had pressed the lever ($M = 1.95$, $SD = 1.15$) compared to trials when they had not pressed ($M = 1.52$, $SD = .38$), $t(9) = 1.49$, $p = .17$. The similarity between these two types of trials suggests that rats were able to search with equal accuracy regardless of whether they were using information collected from the signal light or information present in reference memory.

The graphical representation for the lever pressing behaviour measured in Phase 2 of Experiment 2 can be viewed in Figure 4. Figure 4 presents these data when coded using the “Press First” coding procedure. In this case, rats pressed the lever before completing any searches to maze arms on 30% of trials at the start of the phase. During the duration of Phase 2, the likelihood that they would lever press in this manner rose to about 45% of trials. Figure 4 also presents the same data coded using the “Press Ever” coding procedure. Using this approach, rats were pressing the lever at some point during a trial on 50% of trials when they began Phase 2. The lever pressing behaviour measured in the rats had increased to include approximately 65% of trials by the completion of the phase.

After completing Phase 1 of Experiment 2, rats were placed back on the Experiment 1 procedure (Phase 2) in order to perform a reversal procedure in which rats should track the informative value of the signal light and recover lever pressing. To test for effects of the random-arm procedure, a repeated-measures analysis of variance was performed on both the Press First and Press Ever datasets. No significant effect of session was found in the Press First dataset, $F(19, 171) = 1.34$, $p = .28$. The Press Ever data also showed no effect, $F(19, 171) = 1.11$, $p = .37$.

Although no significant effects of session on lever pressing in Phase 2 were found, a more direct comparison was used to assess whether or not rats were performing the lever pressing behaviour differently between the completion of Phase 1 (in which the food was hidden in the same spatial location) and the completion of Phase 2 (in which the rats could not predict the location of the hidden food). A paired-sample t-test was used to compare the pressing behaviour observed during the last three sessions of Phase 1 and the last three sessions of Phase 2 for both the Press First and Press Ever datasets. The analysis of the Press First dataset found no significant differences between the pressing behaviours in Phase 1 ($M = 33.3\%$, $SD = 4.03$) and Phase 2 ($M = 46.7\%$, $SD = 4.00$; $t(9) = -1.72$, $p = .12$), suggesting that the rats were pressing the lever before performing any searches to maze arms on an equal number of trials in Phases 1 and 2. The analysis was repeated using the Press Ever dataset. Results indicated that the rats pressed the lever at any point during a trial significantly more often during Phase 2 ($M = 65.6\%$, $SD = 3.4$) than during Phase 1 ($M = 34.4\%$, $SD = 4.0$; $t(9) = -3.02$, $p = .02$), suggesting that, overall, rats made lever pressing responses significantly more often on trials in which they could not predict the location of a hidden reward (Phase 2) than when they could use a reference memory to determine the location of a hidden reward (Phase 1).

Figures 5 and 6 present the searching behaviour observed in Phase 2 of Experiment 2. Figure 5 shows the average number of searches required for rats to find the hidden food reward in this phase. Rats completed approximately three searches to maze arms at the beginning of Phase 2, and this value decreased to slightly more than two searches per trial by the conclusion of the phase. To determine if lever pressing improved search performance, the number of searches completed in trials in which a lever press had been performed was compared to the number of searches completed in trials without a lever press. Figure 6 presents this comparison. Overall, rats required 3.29 searches to find the hidden reward on trials in which they had pressed the lever. On trials without a lever press, rats required 3.46 searches to find the hidden reward.

A repeated-measures analysis of variance was performed on the average number of searches made on all trials in Phase 2 to determine if the observed searching behaviour changed significantly during the phase. Session did not affect the rats' searching behaviour ($F(19, 171) = 1.47$, $p = .22$), suggesting that rats maintained stable searching performance during Phase 2. A paired-sample t-test was then performed to determine if the number of searches rats required on trials in which they had pressed the lever was different than the number of searches they required on trials when they had not pressed the lever. Results found that rats required slightly fewer searchers to find the hidden food on trials when they had pressed the lever ($M = 3.29$, $SD = 1.49$) than on trials when they had not pressed the lever ($M = 3.46$, $SD = 1.56$), but this difference was not significant

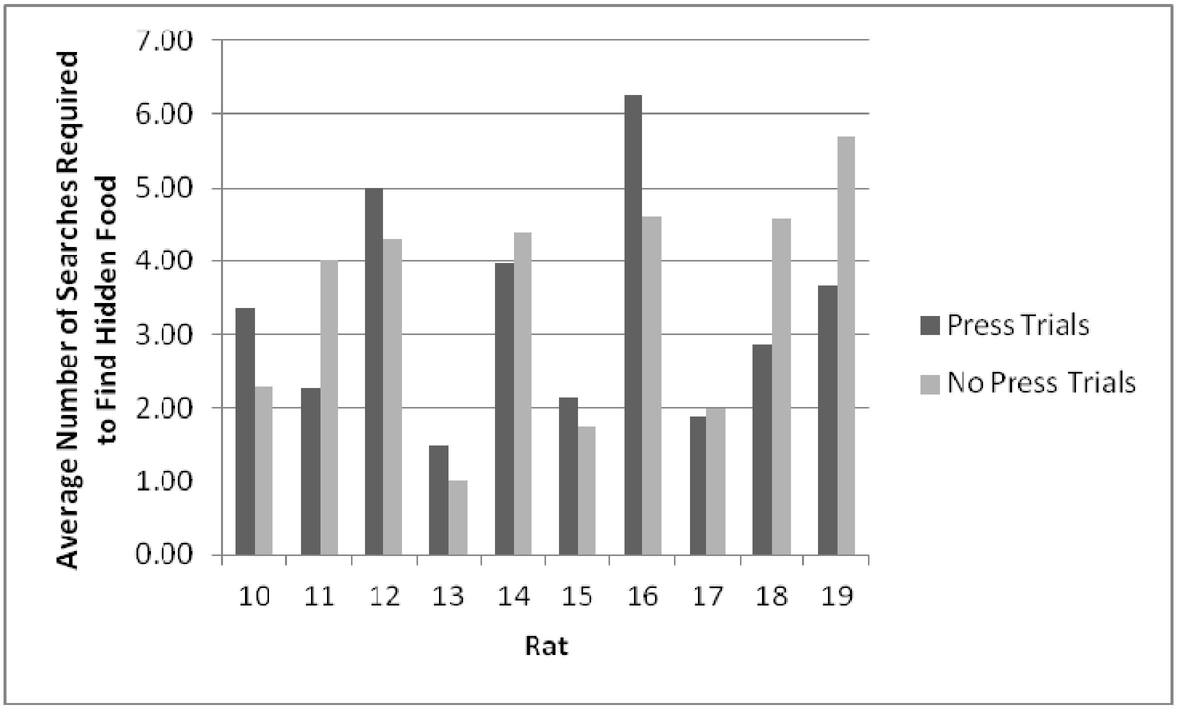

Figure 6: Graphical representation of the number of searches required by rats to find the hidden food on trials in which they completed a lever press and on trials in which they did not complete a lever press in Experiment 2 Phase 2. On average, rats required 3.29 searches on trials with a lever press, compared to 3.46 searches on trials without a lever press.

(*t*(9) = -.42, *p* = .68), suggesting that rats were not efficiently employing information obtained from the signal light (received after lever pressing) to improve their searching efficiency during Phase 2.

Discussion

In Experiment 2, the location of food on the maze did not change, and, after some experience, rats formed a reference memory for the location of the food reward (Phase 1). This reference memory rendered the information provided by the signal light as unnecessary because the rat already had information in memory of where the food was located. I wanted to know if rats were aware that this information already existed in memory and if they could use this knowledge state to alter their lever-pressing behaviour. Results showed that for both the Press First and Press Ever coding methods, rats significantly decreased their lever pressing in response to the location of food remaining the same. These findings suggest that rats were aware that they already knew the location of food and, in response, stopping asking to see the signal light by decreasing their lever-pressing behaviour. Coupled with the findings from Experiment 1, this suggests that rats are aware of what they know and what they do not know and can change their information-seeking behaviour accordingly.

With respect to searching behaviour, the statistical analysis found that rats did not significantly change the number of searches they required to find the hidden food reward during Phase 1. Although the rats had experienced a change in the procedure (the food was always found in the same spatial location during this phase) the change did not affect their ability to find the hidden reward with a minimal amount of searches. Further analysis of the searching behaviour found that rats searched equally well on trials in which they had pressed the lever and on trials in which they had not, suggesting that rats were able to use information stored in reference memory as efficiently as information collected from the signal light.

Experiment 2 also featured a reversal procedure in which rats were placed back on the Experiment 1 random-arm procedure (Phase 2). The purpose of this reversal was to test how flexibly the rats could respond to changes in information pertinent to a particular trial. My hypothesis stated that rats should recover their lever pressing because they could no longer predict the location of food using their reference memory. Although lever pressing increased in Phase 2, repeated-measures analyses of variance for both the Press First and Press Ever coding methods found that rats did not significantly increase their lever pressing within sessions using the reversal procedure.

Because rats may have rapidly reverted to a no-information strategy in Phase 2, a second analysis was used to study the lever pressing behaviour observed in Phase 2 of Experiment 2. A comparison was made between the lever pressing behaviour measured in the final three sessions of Phases 1 and 2 to determine if rats produced significantly different amounts of lever pressing behaviour. A paired-sample t-test found that rats performed lever presses at some point during a trial (Press Ever dataset) significantly more often when they could not predict the location of food on a trial (Phase 2) than on trials in which they had a reference memory for the location of the hidden reward (Phase 1). These findings suggest that rats are indeed sensitive to the presence or absence of information in memory and that they can alter their information-seeking behaviour based on this knowledge state.

A repeated-measures analysis of variance concerning the number of searches that rats performed to find the hidden food in Phase 2 found that this searching behaviour did not change significantly throughout the duration of the phase; overall, rats produced stable searching behaviour. However, the mean number of searches that the rats completed in Phase 2 appeared higher than in Phase 1. To further investigate why this was the case, trials were divided into those that contained a lever press and those that did not. A paired-sample t-test found that rats searched with equal proficiency regardless of whether they had pressed the lever or not. Two conclusions can be drawn from this result. The first is that the overall increase in the number of searches that rats completed in Phase 2 was driven by a decrease in searching accuracy on those trials in which a lever press had been completed. Overall, rats required less searches to find the hidden food on trials in which the lever had been pressed than on trials in which the lever had not been pressed, but this difference was not significant. Second, when the lever was pressed, some rats may not have been able to use information gathered from the signal light to complete the searching portion of the task at a high level of accuracy. Because Phase 1 of this experiment resulted in a decrease in lever pressing behaviour across all rats, it is possible that some rats experienced a reduction in proficiency with using the signal light to complete searches due to the length of time that had passed since the rats regularly encountered the signal light. Specifically, the reduction in proficiency with the signal light could be driven by the fact that some rats did not respond to view the signal light for close to three weeks (the duration of Phase 1 of Experiment 2) and therefore the rats' memory for the light as a signal in Phase 2 may have degraded. Rats may have also experienced retroactive interference during Phase 2: in Experiment 1, rats improved their reinforcement outcomes by obtaining the signal light, but in Phase 1 of Experiment 2, rats inhibited responses to the lever. These behavioural changes may have resulted in an overall decrease in the recovery of lever pressing behaviour measured in Phase 2.

Experiment 3

Experiments 1 and 2 provided evidence that rats will respond for information when it is needed to solve a task and that they will stop responding for information when the answer to a problem is already known. Results from a reversal procedure performed in Experiment 2 also suggest that rats can respond flexibly to changes in the need for information within a task. Experiment 3 asks whether rats are sensitive to the amount of information obtained by a lever press. Rats were presented with trials on which they could obtain four amounts of information. I was interested in rats' ability to discriminate among these levels of information and whether information-seeking behaviour would increase as amount of information increased, similar to the work done with orangutans by Marsh and MacDonald (2012b). They presented orangutans with trials in which a food reward could be hidden beneath one of two, three, or four opaque cups that were placed on top of a clear Plexiglas shelf. Orangutans could perform an information-seeking behaviour by bending down and looking up through the Plexiglas shelf to view where the reward was hidden. Results showed that the orangutans performed more of these information-seeking behaviours as the number of opaque cups (potential locations where the food reward could be hidden) increased.

In order to vary the amount of information that the rats received for completing a lever press, the number of open maze arms was controlled using the guillotine doors present on the maze. Rats encountered trials in which one, two, four, or eight arms were available to search. The amount of information provided by the signal light can be quantified as bits of information. Because only one of the open arms was correct for each trial, trials were more difficult to complete as the number of open arms increased. For example, if a rat was placed on the maze with one arm available to search and the remaining seven arms blocked by the guillotine doors, the rat had a 100% chance of choosing the correct arm on its first search because there were no other locations to search. Therefore, if the rat were to press the lever on this trial, it would receive zero bits of information because the signal light would not offer new information concerning the location of hidden food for that trial. If this same rat entered the maze and found that two arms were available to search, it would then stand a 50% chance of choosing the correct arm on its first search, were it to search at random. If the rat performed a lever press at this time, it would receive one bit of information concerning the location of the hidden food. The likelihood of choosing correctly on the first search falls even farther (to 25%) on trials in which four arms are available to be searched, and a lever press would provide two bits of information about the location of hidden reward. Finally, if all eight arms on the maze are open to be searched, a rat stands a 12.5% chance of choosing the correct arm on the first search. A lever press then provides three bits of information about the location of hidden food.

In the current experiment, rats were allowed to make as many responses as necessary to choose the correct arm. Order of trial difficulty was randomized, and, to mitigate the effects of procedural changes, rats were given five sessions of training on each trial difficulty before experiencing the five sessions of testing. It was hypothesized that a subject with metacognition should increase information-seeking behaviours as the number of open arms (information) increased. This experiment also tests if rats will inhibit information-seeking when they already know the location of food, but in a novel way. In Experiment 2, rats learned over time that food was always hidden in the same location and, in response, decreased their lever-pressing behaviour. In Experiment 3, one condition featured only one arm available to search. A rat with metacognition should reason that food must be hidden on the only available arm and, therefore, refrain from performing a lever press to gain information which is redundant.

Methods

Animals. The rats used in Experiments 1 and 2 were used for Experiment 3.

Apparatus. The radial maze used in Experiments 1 and 2 was used in Experiment 3. However, in this experiment, an additional portion of the maze was utilized. Wooden frames, measuring 30 cm high, above the entryway to each of the eight arms held an opaque wooden guillotine door. Each door could be independently raised and lowered by a pulley system consisting of fishing line and a control panel on an adjacent wall of the testing room. Lowering a door blocked the subject’s access to that arm; this allowed the experimenter to vary the number of arms available to a rat on a particular trial.

Procedure. In Experiment 3, rats could experience trials with one, two, four, or eight arms open to search. All rats received 10 sessions with each number of open arms, totaling 40 sessions for Experiment 3. Sessions were blocked so that each rat experienced sessions of one type for 10 days before moving to the next type, and the order of the conditions was counterbalanced across rats (e.g., Rat 1 received 10 sessions with one arm open, then 10 sessions with two arms, then four, and then eight, while Rat 2 received 10 sessions with four arms open, then 10 sessions with one arm, then eight, then two, and so on). The first five sessions of a block were considered training so that the rats could adjust to the procedural changes; data from these days were not included in the analysis. Sessions six through 10 for each rat for each block formed the dataset to be analyzed for this experiment. Individual trial procedure matched that of Experiments 1 and 2: a trial began when the rat was placed in the hub, all searching or lever pressing behaviours were recorded, and the trial ended when the correct arm was chosen. A random number generator was used to randomize which arms were closed, which were open to be searched, and which arm was correct so that every trial featured a different combination of arms for the rat to explore.

Results

As in Experiments 1 and 2, data for Experiment 3 were coded in such a way that both Press First and Press Ever datasets were created. Both of these datasets were analyzed using a split-plot analysis of variance, using condition (indicating how many arms were open on a trial) and session (signifying the individual sessions within a block of each condition) as within-subject variables. The order in which rats received the different condition types served as a between-subjects variable.

Figure 7 presents the lever pressing behaviour observed in the four conditions for Experiment 3. Figure 7 represents the Press First dataset. Trials were coded as containing a lever press only when that press occurred before any searches were completed to arms of the maze. Figure 7 also shows the same data recoded using the Press Ever coding procedure. Trials containing a lever press at any point before the hidden food was found were counted as containing a lever press. Both figures show an

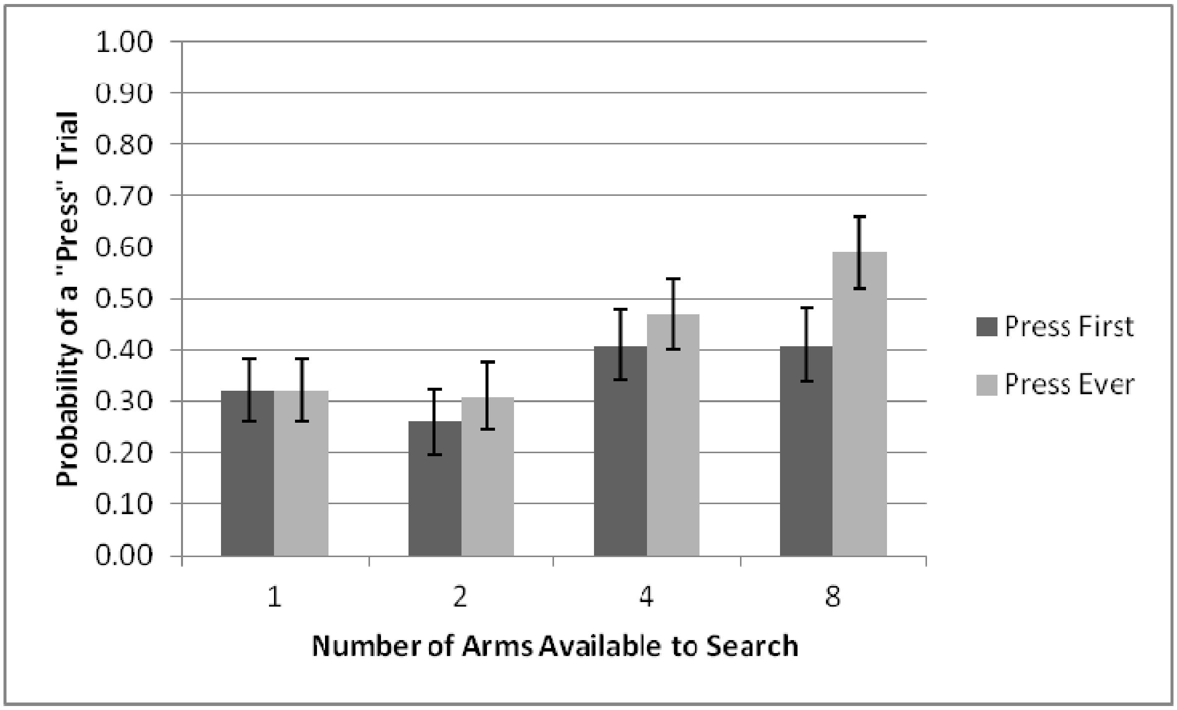

Figure 7: Graphical representation of lever pressing behaviour for the Press First and Press Ever datasets in Experiment 3.

increase in lever pressing between the one and two arms available and the four and eight arms available conditions.

For the Press First dataset, a significant condition by order interaction was found, $F(9, 18) = 3.19$, $p = .03$. No main effects of condition, $F(3, 18) = .55$, $p = .61$, or order, $F(3, 6) = 2.38$, $p = .17$, were found. The interaction was driven by differences between the four orders. Two of the orders (4, 1, 8, 2 and 1, 2, 4, 8) were performed similarly to each other across the four conditions, demonstrating a decrease in lever pressing as the number of open arms increased. This pattern of behaviour is in direct opposition to the other two orders (2, 8, 1, 4 and 8, 4, 2, 1), both of which showed an increase in lever pressing as the number of open arms increased. In terms of the aims of this program of study, this was not a meaningful interaction. Sessions within each condition did not have a significant effect on lever pressing behaviour, $F(4, 24) = 2.86$, $p = .08$.

Analysis of the Press Ever dataset yielded no significant effect of condition, $F(3, 18) = 1.76$, $p = .22$, and no significant effect of session, $F(4, 24) = 2.39$, $p = .13$. Additionally, order was found to have no effect on lever pressing behaviour, $F(3, 6) = 2.31$, $p = .18$. Results indicated that the Experiment 3 procedure had no effect on rats' likelihood to make a lever-press response.

Figures 8 and 9 display the searching behaviour observed in Experiment 3. Figure 8 presents the average searches performed across all trials for each of the four conditions. For the condition in which one arm was open for rats to search, all rats found the hidden food on the first search. For the conditions with two and four arms open per trial, the rats required slightly more searches on average to find the hidden food (1.43 and 1.74 searches, respectively). Finally, rats that required the most searches to find the

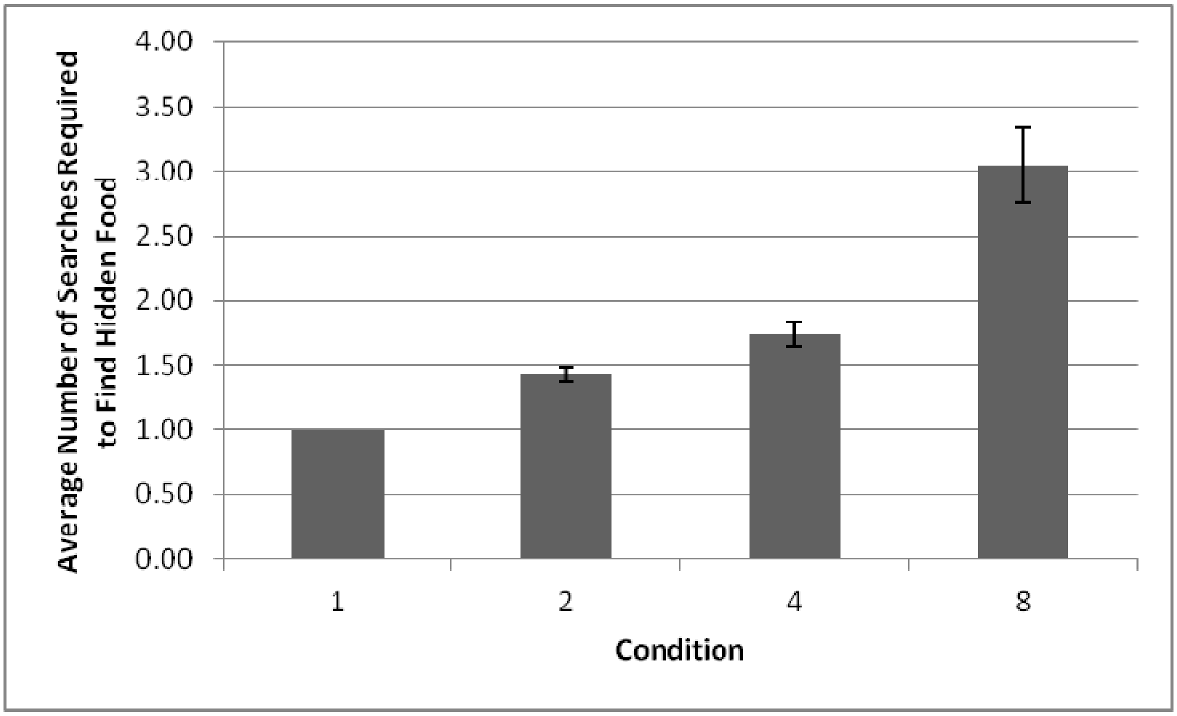

Figure 8: Graphical representation of searching behaviour on all trials in Experiment 3.

hidden food in the eight arm condition completed an average of approximately three searches per trial. Figure 9 presents the same search data divided into trials which contained a lever press and trials which did not for each condition. The figure illustrates that rats always searched more accurately on trials in which they had pressed the lever; this is especially true for the eight arm condition in which trials with a lever press required approximately 2.5 searches, while trials without a press required almost four searches.

To examine the searching behaviour observed in Experiment 3, a repeated-measures analysis of variance was performed on the data presented in Figure 8. Results showed that the rats' searching behaviour changed significantly based on the number of maze arms that were available to be searched, $F(3, 27) = 13.44$, $p = .004$. To determine how conditions differed from one another, pairwise comparisons were conducted using Bonferroni adjusted alpha levels. Results indicated that the number of searches required for the one-arm condition ($M = 1$, $SD = 0$) was significantly lower than the number of searches required for the two-arm condition ($M = 1.43$, $SD = .071$), $p = .001$. The one-arm condition also differed significantly from the four-arm condition ($M = 1.73$, $SD = .07$) at $p = .002$ and from the eight-arm condition ($M = 3.05$, $SD = .500$) at $p = .016$. Further pairwise comparisons indicated that the two-arm condition was not significantly different than the four-arm condition ($p = .20$) but significantly differed from the eight-arm condition at $p = .049$. The search behaviour observed in the four-arm condition was not significantly different than that observed in the eight-arm condition ($p = .08$). No main effect of session was observed, suggesting that rats maintained stable searching behaviour across the five sessions of testing.

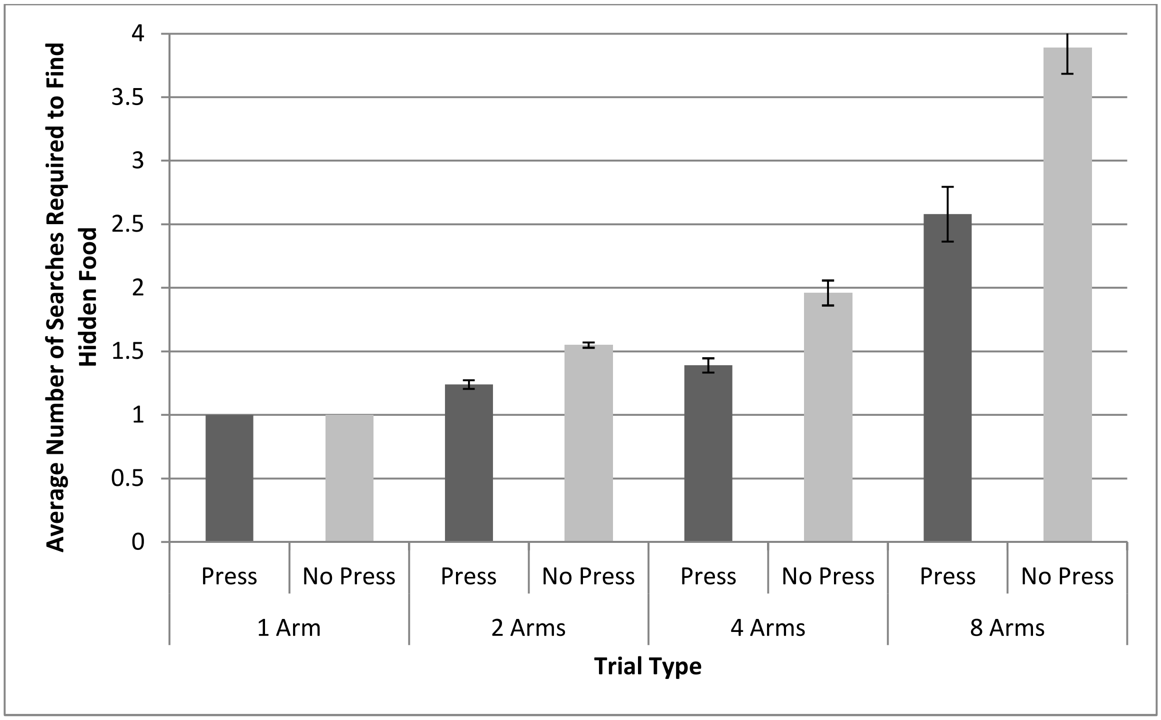

Figure 9: Graphical representation comparing searching behaviour on trials with and without a lever press in Experiment 3.

In order to examine whether rats employed the information provided by the signal light to improve their searching behaviour, trials were divided into those that contained a lever press and those that did not (illustrated by Figure 9). For both trial types, data were collapsed across sessions for each rat, in all four conditions (one arm open, two arms open, etc.). There were some cases of missing data: for example, one rat pressed the lever on all trials in which eight arms were available to search, and therefore did not have a score for the number of searches required for the eight-arm condition without a lever press. Missing data were replaced using mean substitution to avoid removing the subject from the analysis entirely. Conclusions drawn from data replaced using mean substitution should be interpreted with caution, as this method of handling missing data can inflate the likelihood of committing a Type 1 error. The analysis showed a significant interaction effect between the number of arms that were available to search and whether or not the trial contained a lever press, $F(3, 27) = 6.76$, $p = .013$. The disparity between the number of searches performed on trials with a lever press and on trials without a lever press increases as the number of arms available to search increases, which drives the observed interaction. The number of arms available to search was found to have a significant effect on the average number of searches, $F(3, 27) = 28.20$, $p < .001$. Pairwise comparisons using Bonferroni adjusted alpha levels were conducted to determine how conditions differed from one another. The one-arm condition ($M = 1$, $SD = 0$) was found to differ significantly from the two-arm condition ($M = 1.40$, $SD = .04$) at $p < .001$, from the four-arm condition ($M = 1.68$, $SD = .13$) at $p = .003$, and from the eight-arm condition ($M = 3.24$, $SD = .37$) at $p = .001$. There was no difference between the two-arm and four-arm conditions ($p = .24$), but the two-arm and eight-arm conditions significantly differed at $p = .005$. Finally, the four-arm condition was found to be significantly different from the eight-arm condition, $p = .005$. A significant main effect was found such that trials in which the rats had pressed the lever had fewer searches to maze arms than trials where no lever press was completed, $F(1, 9) = 18.73$, $p = .002$.

Discussion

The current experiment attempted to test rats' sensitivity to the amount of information they could gain by pressing a lever and receiving a signal light. Rats were exposed to four conditions in which one, two, four, or eight arms of the maze were available to search. For each trial, one arm was correct, and the location of this arm changed from trial to trial. Rats gained no information when pressing the lever when one arm was available to search because it could be deduced that the reward was hidden on the single available arm. For trials in which two arms were available, rats gained one bit of information concerning the location of the food by pressing the lever. Rats gained two bits of information when four arms were available to search. Finally, on the most difficult condition in which all eight arms were available to be searched, rats gained three bits of information by responding to illuminate the signal light. I was interested in whether rats could track the increasing difficulty of these conditions and alter their information-seeking behaviour accordingly; that is, I hypothesized that rats would be more likely to press the lever and receive the signal light indicating the location of food as the trial difficulty and information gained increased. All rats received all four conditions.

A split-plot analysis of variance of the Press First dataset found a condition (within-subjects variable) by order (between-subjects variable) interaction, indicating that a rat's performance on a particular condition varied depending on the order in which it received the four conditions. Although lever pressing probability increased as number of open arms increased, no main effect of condition was found for this data set, implying that rats' lever-pressing behaviour did not significantly change in response to the different conditions. The null effect of order indicated that the order in which rats received the four conditions did not significantly influence their lever pressing. Finally, session was not found to have an effect, suggesting that rats did not change their responding based on how many sessions of a particular condition they had completed.

A split-plot analysis of variance of the Press Ever dataset produced similar results. A null effect of condition (within-subjects variable) implied that rats did not change their behaviour in response to the varying levels of difficulty of the four conditions. The order in which rats received the conditions (between-subjects variable) did not affect their lever-pressing behaviour, nor was there an effect of session (within-subjects variable).

The searching behaviour performed by rats in Experiment 3 was analyzed using a repeated-measures analysis of variance. Results indicated that rats produced significantly different numbers of searches depending on how many maze arms were available for them to search. Specifically, rats completed significantly fewer searches on trials in which only one maze arm was available than on any other condition type, likely indicating a floor effect, as rats were able to immediately proceed to the location of the hidden reward because no other arms were available to be searched. Results also found that the two-arm condition was significantly different from the eight-arm condition, but not the two-arm condition, suggesting that rats were able to search with a similar accuracy rate in the two- and four-arm conditions, but required more searches with all eight arms open. Similarly, the number of searches completed in the four-arm condition did not differ from the number completed in the eight-arm condition, suggesting that rats were searching with similar proficiency in these two conditions. It appears that rats maintained stable searching behaviour throughout the duration of testing, as session number was not found to have an effect.

After the completion of this analysis, search behaviours were divided into trials that contained a lever press and those that did not, in order to understand if the presence or absence of the information provided by the signal light affected the rats' searching behaviour. An analysis of variance indicated a significant interaction between the number of open arms and the occurrence versus non-occurrence of a lever press. Although the number of searches completed on trials when the lever was pressed remained low, the number of searches performed on trials without a lever press grew as the number of open arms increased, producing the observed interaction. A main effect of the number of open arms was found. Pairwise comparisons found that the one-arm condition required significantly fewer searches than the other three conditions. As with the previous analysis, this is likely representative of a floor effect that bolstered rats' searching accuracy. The two-arm and four-arm conditions were not found to be significantly different in the number of searches that rats performed. However, both of these conditions were significantly different from the eight-arm condition, implying that the eight-arm condition required significantly more searches to find the hidden food than any other condition. Importantly, a main effect was found indicating that rats required significantly fewer searches to find the hidden food when they had pressed the lever than on trials in which they did not press, suggesting that rats were making use of the information provided by the signal lights to improve the efficiency of their searching on the maze.

My hypothesis for Experiment 3 was not supported: rats did not show significant sensitivity to the amount of information to be gained by responding for a signal light on a particular trial. One explanation for this finding is that rats were not able to distinguish between these levels of information. However, this seems unlikely when compared to the results from Experiments 1 and 2, which suggested that rats could distinguish between the presence or absence of information in their memory. An alternative explanation is that rats may not have been motivated to attend to each trial and use memory monitoring to alter future behaviour. In this experiment, rats were permitted to make as many searches as were necessary to find the food reward. All trials ended with the rat receiving food reinforcement, regardless of the efficiency of a rat's searching behaviour. Motivation could be increased if incorrect searches became costly. In Experiment 4, the procedure was altered so that rats could make only one search per trial in order to address this alternative explanation for the rats' behaviour in Experiment 3.

Experiment 4

In Experiment 3, I aimed to examine rats' sensitivity to changes in the amount of information they could gain by performing the lever-pressing behaviour. The effects were found to be weak, and it appears that rats may have difficulty judging between different levels of information. The purpose of Experiment 4 was to increase rats' motivation to appropriately alter their behaviour in response to these information changes. Rats were allowed to make only one choice per trial; the trial terminated after the rat had entered an arm of the maze. This procedural change greatly increased the cost of making an incorrect choice, as incorrect responses resulted in no reinforcement for that trial. The experimental design for this study matches that used in Experiment 3 in every other aspect. Additionally, this procedure forced rats to decide whether to respond for information at the beginning of the trial instead of allowing them to seek help partway through their search.

Methods

Animals and Apparatus. The rats used in Experiments 1, 2, and 3 were used in Experiment 4. All aspects of the maze employed in Experiment 3 were also used in Experiment 4.

Procedure. In Experiment 4, the procedure was identical to that of Experiment 3, with the exception that rats were only allowed to enter one maze arm per trial. Trials ended as soon as the rat made a choice, and the guillotine door was lowered so that the rat could not return to the hub and make a subsequent search, for both correct and incorrect choices.

Results

In the previous three experiments, data were coded in two ways to produce a Press First and a Press Ever dataset. Both datasets were then analyzed in the same manner and results were reported. For Experiment 4, data were coded using the Press First method because rats were permitted only one search per trial and could not return to the hub and complete a subsequent lever press.

The lever pressing behaviour observed in Experiment 4 is presented in Figure 10. Overall, the likelihood that rats would complete a lever press in this experiment was low. Rats pressed the lever on approximately 18% of trials with one, two, and four arms

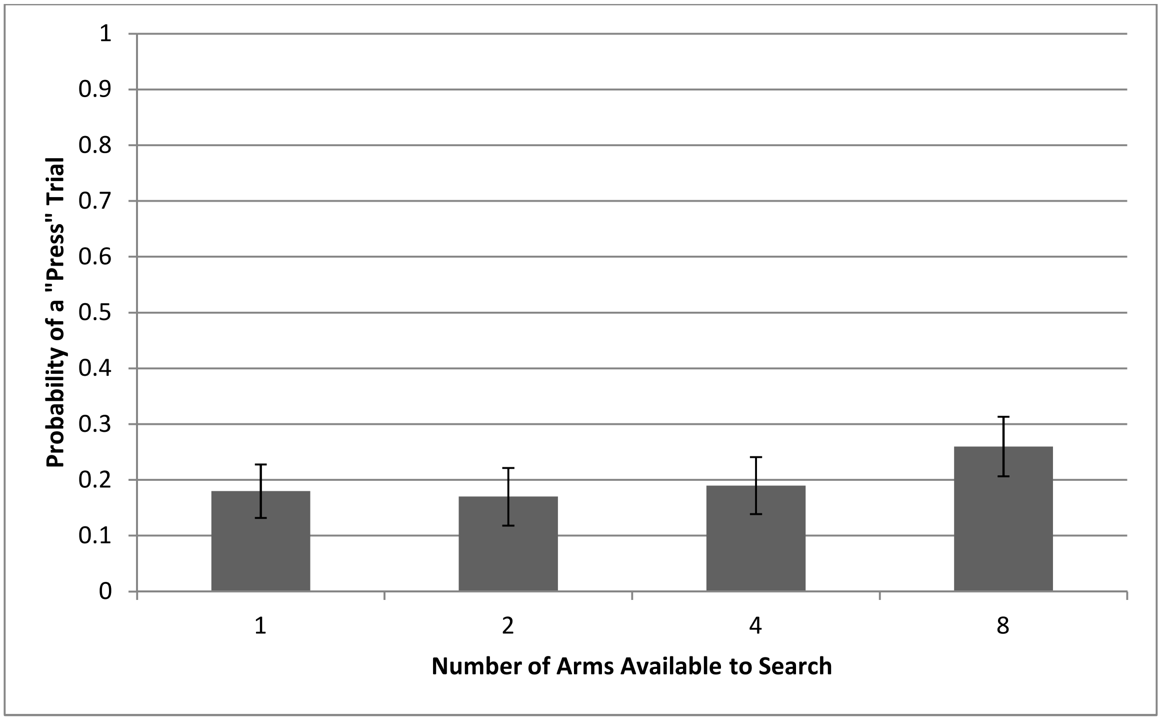

Figure 10: Graphical representation of lever pressing behaviour observed in Experiment 4.

available to search. This probability rose slightly for the eight-arm condition, with rats pressing the lever on approximately 25% of trials.

A split-plot analysis of variance investigated the effects of the procedure on the likelihood that rats would perform a lever press, using condition and session as within-subjects variables and order as a between-subjects variable. Condition type, meaning the number of arms available for a rat to search, was found to have no significant effect, $F(3, 18) = 1.00$, $p = .40$. Additionally, no effect of session was found, $F(4, 24) = .73$, $p = .51$. Finally, the order in which rats received the four conditions did not affect their propensity to press the lever, $F(3, 6) = 1.29$, $p = .40$. These results suggest that the Experiment 4 procedure had no impact on rats' likelihood to lever-press for information about the task.

The searching behaviour observed in Experiment 4 is displayed in Figure 11. Rats were permitted to make one search per trial. Unlike the previous three experiments, if rats did not choose the correct arm for a trial on their first search then they received no reward for that trial. Figure 11 shows the percentage of trials in which the rats were reinforced, indicating that they chose the correct arm on their first search. In some instances, data were not available for all conditions for all rats (for example, one rat never pressed the lever for the two arm condition and so no score was obtained for searching proficiency in this condition). In order to mitigate data loss due to removing these subjects from the analysis, missing data were replaced using mean substitution. Because this statistical approach can inflate the likelihood of committing a Type 1 error, conclusions from this analysis should be interpreted with caution.

A repeated-measures analysis of variance was performed to study the searching behaviour observed in Experiment 4. A significant interaction was found between the

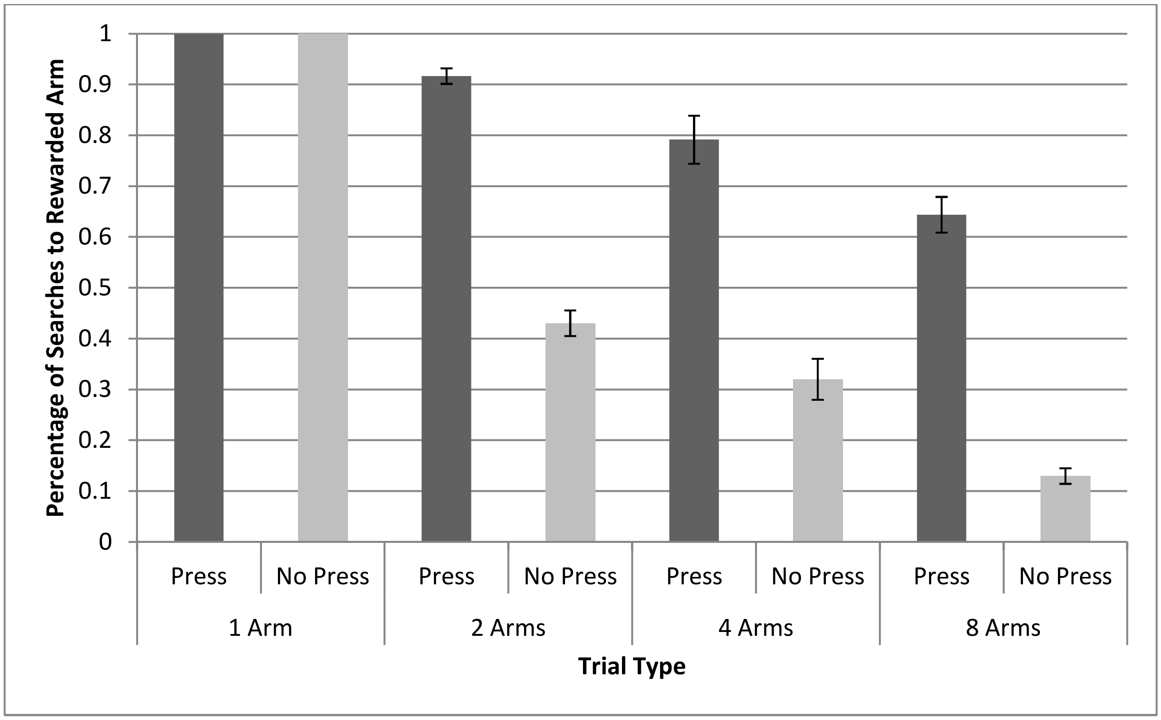

Figure 11: Graphical representation of searching behaviour in Experiment 4.

number of arms available to search and whether or not the rats pressed the lever, *F*(3, 27) = 10.68, $p = .003$. This interaction is driven by the high number of incorrect trials completed by the rats when they did not press the lever. As the number of arms increased the accuracy on both press and non-press trials declined, but the accuracy of the non-press trials decreased at a much faster rate. A significant main effect of condition was observed, *F*(3, 27) = 46.88, $p < .001$. Pairwise comparisons using Bonferroni adjusted alpha levels were performed to further investigate the main effect of condition. Results indicated that the one-arm condition (*M* = 1, *SD* = 0) differed significantly from the two-arm condition (*M* = .68, *SD* = .04) at $p < .001$, from the four-arm condition (*M* = .56, *SD* = .06) at $p < .001$, and from the eight-arm condition (*M* = .39, *SD* = .04) at $p < .001$. The two-arm condition also differed significantly from the eight-arm condition, $p < .001$. The two-arm and four-arm conditions were not found to be different, nor were the four-arm and eight-arm conditions. Finally, a significant main effect of whether or not the lever was pressed during the trial was found (*F*(1, 9) = 127.13, $p < .001$), indicating that rats chose the correct arm significantly more often on trials when they had pressed the lever than on trials when they had not.

Discussion

In Experiment 4, rats experienced four conditions in which they could gain varying amounts of information. To complete a trial, they were required to find a food reward hidden on one arm of the maze. Conditions presented one, two, four, or eight arms that were available to search, and trial difficulty increased as the number of open arms increased. The purpose of this study was to test the rat's sensitivity to the change in amount of information to be gained. In Experiment 4, as in Experiment 3, rats were permitted to make only one search per trial in an attempt to increase their motivation to attend to each trial and perform a correct search.

As rats were allowed only one search, coding of the data was completed using only the Press First method. Results of a repeated-measures analysis of variance indicated no effect of condition, meaning that rats' lever-pressing behaviour did not change significantly in response to the amount of information that could be gained in a condition. Additionally, there was no effect of session, suggesting that the rats' behaviour did not change depending on how many sessions they completed for each condition type. Finally, no effect of order was found, indicating that rats did not vary from one another on the basis of the order in which they received the four condition types.

An analysis of variance performed on the searching behaviour found a significant interaction between condition (number of arms open to be searched) and whether or not the rats pressed the lever on a trial. This interaction illustrated the precipitous drop in searching accuracy as the number of open arms increased on trials when rats did not press the lever. Overall, rats were able to maintain a high level of searching accuracy on trials in which they had pressed the lever. A main effect of condition was observed. Pairwise comparisons found that the one-arm condition showed significantly higher search accuracy than all other conditions; however, this represents a ceiling effect because rats were not able to make a mistake in this condition. The two-arm condition was also found to be significantly different from the eight-arm condition. Lastly, trials in which the lever was pressed were found to have significantly higher search accuracy than trials in which the lever was not pressed, suggesting that rats were able to make use of information gathered from the signal light when completing their searches on trials in which they had pressed the lever.

In Experiment 3, my hypothesis that rats could change their information-seeking behaviour appropriately in response to varying amounts of information to be gained was not supported. I proposed that this could be an artifact of a lack of motivation. Experiment 4 attempted to rectify this by allowing rats to make only one search among the maze arms. Again, my hypothesis was not supported, as the Experiment 4 procedure was not found to affect the likelihood that rats would press the lever to receive information about the task. Rats did not appear to be sensitive to the amount of information they gained by pressing the lever for each condition type.

General Discussion

The previous four experiments investigated aspects of metacognition in the rat. Experiments 1 and 2 provided evidence that rats seek information about the location of hidden food on an eight-arm radial maze. Rats demonstrated this in Experiment 1 by pressing a lever to view a signal light at the end of the arm containing food. Although rats were initially trained to press the lever for an immediate food reinforcer in the hub of the maze, they continued to press the lever for the arm light signal when the immediate reinforcement was discontinued. In Experiment 2, the information provided by the light was made redundant with information contained in the rat's reference memory, because the food reward was placed on the same arm over repeated trials for each rat. In response to this manipulation, rats showed a significant drop in the frequency of lever pressing. However, a higher level of lever pressing was regained in Experiment 2 when the location of the hidden food arm again became random from one trial to the next.

Experiments 3 and 4 explored how sensitive rats were to the amount of information that they stood to gain by lever pressing. Amount of information gained by a lever press was controlled by testing rats on sets of trials in which the correct arm was one of one, two, four, or eight open arms on the maze. Although rats showed an increase in percentage of lever presses as amount of information increased, this change in lever pressing was not statistically significant. These finding suggest that the metacognitive capacity of rats may not be as finely tuned to the amount of information to be gained by an information-seeking response as that of orangutans (Marsh & MacDonald, 2012b) tested in a similar paradigm.

Experiment 1 posed a basic research question: will rats perform a behaviour for information? It is apparent throughout the animal learning literature that rats will learn many behaviours in order to earn a food reward; however, it is not clear if they also value information. In training, rats received an immediate food reward and a signal light (and thereby information) for performing a lever press. In testing, the immediate food reward was withheld and rats only received information concerning the location of hidden food. Rats continued to lever press for the information only, indicating that they understood the importance of the information in completing the task.

There could, however, be an alternative explanation for these findings. It is plausible that the signal lights, which were present in close proximity to the ultimate food reward on the arms, served as secondary reinforcers. Rats might have pressed the lever not for information regarding the hidden food, but for the reinforcing value of the light itself. This possible explanation was tested in Experiment 2. In this procedure, rats found food hidden in the same spatial location on every trial. After some experience, rats developed a reference memory for this location. The information provided by the signal light was now redundant with the reference memory. A rat without metacognition would continue to press the lever in order to receive the reinforcing value allotted by the signal light. A rat possessing metacognition should recognize that its reference memory is sufficient to search accurately and therefore inhibit lever pressing. Results showed that rats significantly decreased their lever pressing in response to acquisition of a reference memory for the location of hidden food, which is critical for two reasons. First, it argues that rats were not lever pressing just to receive a secondary reinforcer in Experiment 1. Second, it demonstrates that rats will terminate information-seeking behaviour when the necessary information already exists in memory.

At the completion of Experiment 2 testing, a reversal procedure was performed. Rats were placed back on the Experiment 1 procedure so that the location of food could not be predicted and only the signal light indicated where food could be found. It was observed that rats recovered their lever pressing in response to this procedural change when the Press Ever data were analyzed. Thus, the results of Experiment 2 suggest that rats were sensitive to whether a lever press provided needed information or not. Lever pressing declined when the light information was not necessary and reappeared when the light information again became necessary.

In Experiments 3 and 4, I studied whether rats would exhibit sensitivity to the amount of information that they could gain by performing a lever press. By having one, two, four, or eight arms open on the maze on different blocks of trials, a lever press yielded zero, one, two, or three bits of information, respectively. I hypothesized that a metacognitive rat would be more likely to press a lever as the amount of information to be gained increased. In Experiment 3, rats were allowed to visit arms until they found the one containing food. Thus, every trial ended with a reward. In order to penalize rats for not responding for information in Experiment 4, only the choice of one arm was allowed. Although the percentage of lever presses increased somewhat with amount of information in both Experiments 3 and 4, the effect of information on lever pressing was not statistically significant. At face value, these findings suggest that rats cannot differentiate between varying amounts of information. Perhaps rats possess a rudimentary form of metacognition in which they can distinguish between the presence or absence of information in memory, but cannot differentiate among these four quantity of information conditions. This explanation is plausible, but does not truly explain the data: rats behaving in accordance with this account should have refrained from pressing the lever in the condition when they gained no information (one arm open), and pressed equally frequently for the other three conditions (two, four, or eight arms open). The statistical analysis, however, revealed no significant differences among the four conditions.

With the overarching conclusions of these studies outlined, it is now appropriate to compare the results of this program of study with other research on metacognition. Foote and Crystal (2007) explored metacognition in rats using the uncertainty paradigm. This paradigm was designed to study how rats monitor information that they hold in memory. They found that rats rejected trials more often as the discrimination grew more difficult and that rats performed better on trials in which they chose to make a discrimination response than on those trials in which they were forced to do so. It was previously argued in this essay that a comprehensive review of metacognition within a species should consider both uncertainty tasks (aimed at the “monitoring” dimension) and information seeking tasks (aimed at the “control” dimension). My findings complement the uncertainty work done by Foote and Crystal (2007) by studying the information-seeking behaviour of the rat. Like them, I found evidence that rats may have access to the states of their own memories. Using a different apparatus, a different procedure, and a different sensory modality (vision instead of audition), my results corroborate what has been previously found.

These findings can also be compared with information-seeking studies using other species. Hampton et al. (2004) used a tube-pulling task to test information seeking in rhesus macaques. They found that the monkeys were significantly more likely to look down tubes for information about the location of a hidden reward when they had not seen the experimenter bait the apparatus, in comparison to trials in which they were allowed to view the baiting. These results map closely onto the information-seeking behaviours observed in Experiments 1 and 2. Hampton et al. (2004) argued that humans are not the only species with awareness of the contents of their own memory. The current experiments, along with the findings from Foote and Crystal (2007), suggest that non-primate mammals may have memory awareness as well, although more research is needed to ascertain how closely rats can monitor the contents of their memory.

Although this program of study contributed to our scientific understanding of metacognition in the rat, there are many questions still unanswered in this area of research. Some of these questions can be answered by making alterations to the design of the current experiments. One suggestion is to use naïve rats for each experiment. I chose to use the same rats for each of the four experiments to avoid retraining new subjects for each task, as the required training was extensive. However, exposing the same rats to a variety of procedures may have affected their behaviour. A second suggestion concerns Experiments 3 and 4. In the current experiments, all rats experienced all four information conditions during Experiments 3 and 4, and the statistical comparison investigated within-subject variability in lever-pressing behaviour. Because the high number of procedural changes that these rats endured may have affected their behavioural sensitivity to information, subsequent studies should randomly assign rats to a certain condition and then make between-subject comparisons regarding their lever pressing. This procedure should ensure less disruption of the rats' behaviour due to rapid changes in testing conditions.

Finally, the results of these experiments raise further questions concerning the metacognitive abilities of the rat. A simple alteration of the current procedure could test if rats will respond to the lever to obtain a reminder of the location of hidden food when their memory trace for this location is weak. To test this question, the opaque guillotine doors on the radial maze should be replaced with transparent guillotine doors. In the first phase of a trial, the rat will be placed in the hub of the maze. All eight guillotine doors will be in the lowered position so that the rat cannot enter any of the maze arms. The correct arm for that trial (where the hidden reward is located) will have its signal light illuminated. Rats will be allowed to view the arms of the maze through the clear guillotine doors for the duration of the encoding interval. The rat will then be removed from the maze for the duration of a retention interval (for example, two minutes). After this interval has elapsed, the rat will be placed back in the hub of the maze to complete the memory test phase of the trial. All guillotine doors will be in the raised position so that the rat has access to all maze arms. Critically, the signal light will not be illuminated at this time. If the rat has retained a strong memory of the location of hidden food, it should proceed to choose that correct arm and receive the food reward. If the rat no longer remembers where the reward is located, it should press the lever to receive a reminder in the form of the signal light, which will again be illuminated on the correct arm. Experimenters will measure the likelihood that the rat will press the lever during this memory test in a variety of testing conditions. For example, the experimenters could hold the retention interval constant and vary the length of the encoding interval to determine if rats press the lever more often for a reminder stimulus after shorter encoding intervals. Experimenters could also hold the encoding interval constant and compare across varying retention intervals in which rats should press the lever more often after the completion of longer retention intervals.

Additionally, there is no experimental data describing how rats behave when the information that they gain by information seeking is not always reliable. To test this, rats could be placed on the Experiment 1 procedure. When the rats respond to the lever, a signal light is illuminated, but this light only predicts the location of food on a percentage of the trials (e. g., informative on 75% of trials but misleading on 25%). The percentage of trials in which the light is informative could be varied to determine how reliable the signal must be in order for the rat to respond for it.

In conclusion, I performed four experiments to investigate several aspects of metacognition in the rat. In Experiments 1 and 2, I found that rats would respond to a lever in order to receive needed information about the location of a hidden food reward, and that the rats inhibited this behaviour when they could instead use a reference memory to locate the reward. These findings serve as evidence for information seeking and metacognition in rats, especially when coupled with previous findings (Foote & Crystal, 2007). In Experiments 3 and 4, I tested whether rats would exhibit sensitivity to how much information they could gain by lever pressing. My results showed that, even when making an incorrect search became costly, rats did not appear to discriminate among different amounts of information to be gained, suggesting that rats may have some limitations on their sensitivity to information. Finally, I have proposed two novel experimental paradigms, one which investigates whether rats will respond for a reminder stimulus when a memory trace is weak, and a second which investigates how reliable an information source must be in order for a rat to respond for it.

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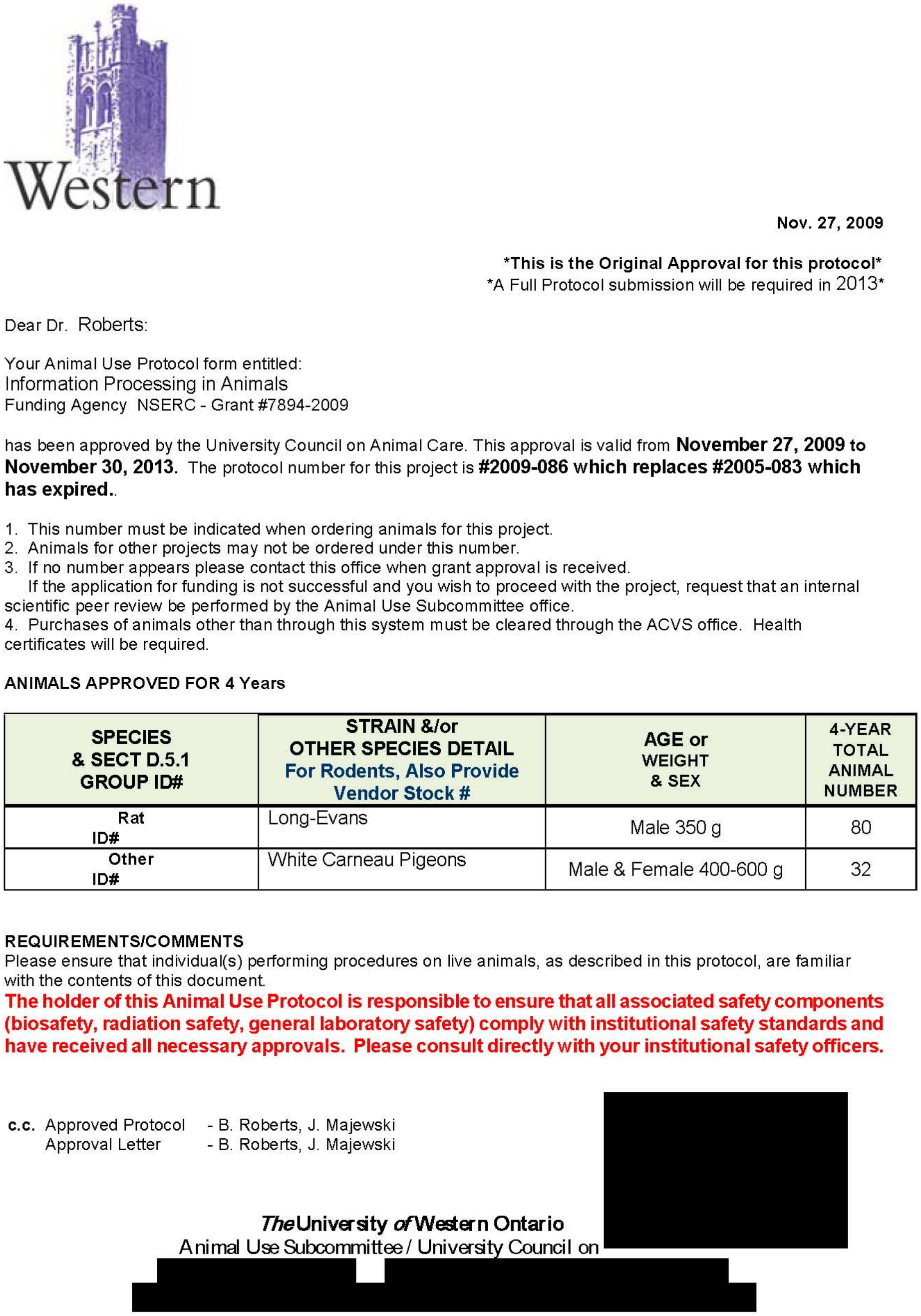
Appendix A – Ethics Approval Form



Western

Nov. 27, 2009

This is the Original Approval for this protocol
A Full Protocol submission will be required in 2013

Dear Dr. Roberts:

Your Animal Use Protocol form entitled:
Information Processing in Animals
Funding Agency NSERC - Grant #7894-2009

has been approved by the University Council on Animal Care. This approval is valid from **November 27, 2009 to November 30, 2013.** The protocol number for this project is **#2009-086 which replaces #2005-083 which has expired.**.

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
   If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

ANIMALS APPROVED FOR 4 Years

SPECIES & SECT D.5.1 GROUP ID#	STRAIN &/or OTHER SPECIES DETAIL **For Rodents, Also Provide Vendor Stock #**	AGE or WEIGHT & SEX	4-YEAR TOTAL ANIMAL NUMBER
Rat ID#	Long-Evans	Male 350 g	80
Other ID#	White Carneau Pigeons	Male & Female 400-600 g	32

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

c.c. Approved Protocol - B. Roberts, J. Majewski
Approval Letter - B. Roberts, J. Majewski

[redacted]

***The* University *of* Western Ontario**
Animal Use Subcommittee / University Council on

[redacted]

Chelsea R. Kirk

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EDUCATION

Master of Science, Behavioural and Cognitive Neuroscience, London, Ontario, 2013
Thesis: Information Seeking in Rats on the Radial Maze
Advisor: Dr. William A. Roberts

Bachelor of Arts, Psychology, University of Kentucky, Lexington, Kentucky, 2011
Thesis: Acquisition of a Simultaneous Mid-Session Reversal in Rats
Advisor: Dr. Thomas R. Zentall

Bachelor of Arts, Sociology, University of Kentucky, Lexington, Kentucky, 2011

HONORS AND AWARDS

May 2013	Nominated for a Graduate Student Teaching Award
Mar. 2013	Third Place for Spoken Presentation, Western Graduate Research Forum
2011-2013	Western Graduate Research Scholarship
2010-2011	University of Kentucky Department of Psychology – Outstanding Psychology Student Award
2008-2009	University of Kentucky Honors Program – Sophomore Award
2007-2011	Presidential Scholarship, University of Kentucky

SERVICE

Mar. 2013	Invited speaker at the 80th Anniversary Ceremony of the Alpha Zeta Chapter of Alpha Phi Omega, a co-ed community service fraternity
Dec. 2012 – June 2013	Member, Disciplinary Investigation Committee, Society of Graduate Students
Aug. 2012 – present	Treasurer, Ontario Ecology, Ethology, and Evolution Colloquium Planning Committee
July 2012 – June 2013	Treasurer, Psychology Graduate Student Association
July 2012 – June 2013	Member of the International Graduate Student Issues Committee, Society of Graduate Students
Jan. 2012 – June 2013	Psychology Councilor for the Society of Graduate Students, University of Western Ontario
June 2010 – May 2011	Treasurer, University of Kentucky Chapter of Psi Chi, International Honors Society in Psychology

June 2010 – May 2011	President, Alpha Phi Omega Co-ed Community Service Fraternity, Alpha Zeta Chapter at the University of Kentucky

TEACHING EXPERIENCE

Sept. 2012 – Apr. 2013	**Lab Instructor**, University of Western Ontario PSY 2820E Research Methods and Statistical Analysis in Psychology
Jan. – Apr. 2012	**Teaching Assistant,** University of Western Ontario PSY 2210 Introduction to Animal Cognition
Sept. – Dec. 2011	**Teaching Assistant,** University of Western Ontario PSY 2800E Research Methods in Psychology
Sept. 16th – 18th 2011	**Teaching Assistant Training Program**, University of Western Ontario Twenty hour training session with micro teaching sessions and feedback from an instructor and a group of peers.

RESEARCH ASSISTANTSHIP

Sept. 2011 – Aug. 2013	University of Western Ontario, Supervisor: W. A. Roberts, Ph.D.
Jan. 2009 – Aug. 2011	University of Kentucky, Supervisor: T. R. Zentall, Ph.D.

PEER-REVIEWED JOURNAL ARTICLES

Rayburn-Reeves, R. M., Stagner, J. P., **Kirk, C. R.**, & Zentall, T. R. (2012). Reversal learning in rats (*Rattus norvegicus*) and pigeons (*Columba livia*): Qualitative differences in behavioral flexibility. *Journal of Comparative Psychology*, *127*(2), 202-211.

Molet, M., Miller, H. C., Laude , J. R., **Kirk, C.**, Manning , B., & Zentall, T. R. (2012). Decision making by humans in a behavioral task: Do humans, like pigeons, show suboptimal choice? *Learning and Behavior*, *40*(4), 439-447.

PRESENTATIONS

Kirk, C. R., Roberts, W. A. (2013, August). Information Seeking in Rats on the Radial Maze. Poster presented at Behaviour 2013, Newcastle, UK.

Strang, C. G., **Kirk, C. R.**, Sherry, D. F. (2013, August). Spatial Memory in Horses. Poster presented at Behaviour 2013, Newcastle, UK.

Kirk, C. R., Roberts, W. A. (2013, March). Information Seeking in the Rat. Paper presented at the Western Graduate Research Forum, London, ON.

Kirk, C. R., Roberts, W. A. (2013, March). Information Seeking in the Rat. Paper presented at the International Conference on Comparative Cognition, Melbourne, FL.

McMillan, N., **Kirk, C. R.**, & Roberts, W. A. (2013, March). Pigeons Make Few Errors on a Variable Mid-session Reversal Task with Visual/spatial Cue Dimensions. Paper presented at the International Conference on Comparative Cognition, Melbourne, FL.

Kirk, C. R., Roberts, W. A. (2012, May). Information Seeking in the Rat. Paper presented at the Ontario Ecology, Ethology & Evolution Colloquium, McMaster University, Hamilton, ON.

Kirk, C.R., Rayburn-Reeves, R., Stagner, J.P., & Zentall, T.R. (2011, May). Within-Session Reversal Learning in Pigeons and Rats. Poster presented at the International Conference on Comparative Decision Making, Lexington, KY.

Kirk, C. R., Rayburn-Reeves, R., Stagner, J. P., & Zentall, T. R. (2011, May). Within-session Reversal Learning in Rats and Pigeons: Comparisons of Behavioral Flexibility. Paper presented at the Center for Ecology, Evolution and Behavior, University of Kentucky, Lexington, KY.

Kirk, C. R., Rayburn-Reeves, R., Stagner, J. P., & Zentall, T. R. (2011, April). Within-session Reversal Learning in Rats and Pigeons: Comparisons of Behavioral Flexibility. Paper presented at the Tri-State (Plus) conference on Animal Learning and Behavior, Purdue University, West Lafayette, IN.

Kirk, C. R. & Zentall, T. R. (2010, October). Acquisition of a Simultaneous Mid-session Reversal in Rats. Paper presented at the Kentucky Honors Roundtable Conference of Undergraduate Research, Western Kentucky University, Bowling Green, KY.