Remember When: The Search for Episodic-like Memory in Animals

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Julia E. Meyers-Manor

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Dedication

This dissertation is dedicated to my loving family, especially my husband Michael.

Abstract

Episodic memory refers to the rich detailed memories of events within a spatio-temporal context. It contrasts with semantic memory which includes context-free representations of facts and general knowledge. Given the frequency and severity of episodic memory deficits in humans, it would be useful to have animal models of episodic memory to better understand and treat the loss of episodic memory in humans. Some researchers have proposed that animals lack the capacity for episodic memory because of the lack of evidence for conscious self-representation in animals. However, many animal researchers have risen to the challenge and devised experiments to test various elements, features, and properties of episodic memory. The literature on episodic memory in animals is reviewed. Then three experiments examined pigeons' memory for *what* events occur, *where* they occur, and *when* they occur. Two additional experiments tested the *flexibility* of these *what-where-when* memories. In Experiment 1, it was shown that pigeons had the ability to track the key location that they had to peck in order to get one of two food outcomes, which changed based on the time of day (morning or afternoon). In Experiment 2, pigeons failed to show that they could use *flexibility* of the *what-where-when* memory found in Experiment 1 in a new transfer-of-control procedure. Experiment 3 and 4 examined the use of *what-where-when* memories in tracking food outcomes, but used how long ago events occurred rather than the time of day. The pigeons were able to use knowledge of how long ago events occurred to choose the keylight location that predicted good food rather than "rotten" or "unripe" food. Finally, in Experiment 5, the pigeons were tested on their ability to flexibly apply knowledge of “ripening” and “rotting” foods from Experiments 3 and 4 to new keylights. As in Experiment 2, the pigeons in Experiment 5 failed to show any evidence of *flexibility* in their *what-where-when* memories. Despite the results of Experiment 2 and 5, the experiments generally suggest that pigeons seem to have the basic elements required for episodic memory but may lack some of the *flexibility* to express those memories.

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Chapter 1: The Puzzle of Episodic Memory in Animals: Assembling the Pieces of a Mind

Episodic memory is a prominent feature of most people's day-to-day experience, but what exactly episodic memory is and is not turns out to be difficult to define. When the capacity for language is removed, the ability to define episodic memory becomes even more difficult. For the past decade, there has been an intense search into the capacity of animals to show episodic memory. There are many aspects of episodic memory that have been tested in animals, using a variety of methods. Each of these endeavors has added elements, features, and properties to our knowledge of episodic memory. As more pieces are fitted into the puzzle of the animal mind, we become more confident in the existence of episodic memory in animals.

The Puzzle of Episodic Memory in Animals: Assembling the Pieces of a Mind

The art and challenge of doing scientific research is often like putting together a jigsaw puzzle. The pieces are all there waiting to be found and assembled into a single, beautiful picture. The challenge is finding all the pieces and getting them into the right spots. As with jigsaw puzzles, some scientific questions are more difficult than others. In studying the animal mind, it often feels like we are trying to make a picture without all the pieces or even the benefit of the “picture on the box”, yet researchers puzzle on. In this paper, we hope to assemble some of the pieces to the puzzle of episodic memory by reviewing the definitions of episodic memory, briefly noting some examples in humans, considering the various pieces of evidence for episodic memory in animals, and finally taking a step back to see the picture that researchers have created so far.

Establishing the Border

Whenever one begins a puzzle, it is always useful to start by creating the border. This clearly defines the location within which all the pieces have to fit. For episodic memory in animals, that means establishing definitions and examples in the human literature.

Tulving (1972) was the first to introduce the term episodic memory. He proposed *episodic memory* and *semantic memory*, as two divisions of a higher order memory system called explicit or *declarative* memory. The early division of these two systems within explicit memory characterized episodic memory as remembered events in spatial and temporal contexts and semantic memory as memory for facts and general knowledge of the world. Tulving defined episodic memory as a system that "receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events" (Tulving, 1972, p. 385). Thus, episodic memory was context dependent and semantic memory was free from context. He also proposed that most early laboratory studies of memory (e.g., memory of word lists) fell into the episodic memory category because they required the participant to recall the occurrence of events in relation to each other temporally or serially; other tests such as the classification of words into categories served to test semantic memory. Empirical evidence from functional, developmental, pharmacological, and brain damage studies has indicated dissociations between semantic and episodic memory in support of Tulving's distinction between these two systems—although they certainly do not imply that the systems are completely independent (for review see Nyberg & Tulving, 1996; see also Graham, Simons, Pratt, Patterson, & Hodges, 2000).

Tulving's original definition shifted in 1983 when he re-envisioned episodic memory in his book *Elements of Episodic Memory*. In this new vision, Tulving emphasized that it was no longer enough to remember spatial and temporal contexts of events in episodic memory but that the experience of the memory also had to involve "*autonoetic consciousness"*. Autonoetic consciousness refers to "the ability of an individual to become aware of his or her own identity and existence in subjective time that extends from the past through the present to the future" (Tulving, 1985a, p. 388). He placed this in contrast to the consciousness involved in semantic memory, *noetic consciousness*. Noetic consciousness is the feeling of knowing that something is true but without an involvement of the self in the remembered event (Tulving, 1985a). Although autonoetic consciousness implies that anything relating to the self would fall under this category of consciousness, Tulving (1985a) distinguishes between semantic knowledge of the self, such as facts about a birth date or the location of houses that one lived in, and episodic memory, which involves *re-experiencing* the past events in one's memory.

Others have followed Tulving's (1983) turn toward an emphasis on the experiential and self-reflective components of episodic memory. Suddendorf and Corballis (1997) suggested that to have episodic memory, an individual needs to have self-awareness, reconstructive imagination, the ability to meta-represent[1] knowledge, and the ability to dissociate one's present mental states from past mental states. Further, they suggest that episodic memory is most important for its capacity to allow future planning. Future planning and episodic memory are thus placed on two ends of a *mental time-travel* spectrum. In both Tulving's (2002; 2005) and Suddendorf and Coraballis' (1997) view of mental time travel, traveling mentally into the future is as important or perhaps even more important than mentally traveling into the past. These two dimensions of time travel are also sometimes called *retrospective* and *prospective memory.* Roediger (1996) described the difference in typical studies of retrospective and prospective memory as a difference in remembering words from a list and remembering lists of things to do. Both types of memory hold many common properties (see Roediger, 1996; Suddendorf & Corballis, 2007) which may indicate that

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[1] Meta-representation refers to the ability to reflect on one's own thoughts, feelings, and knowledge.

they do in fact represent two ends of a mental time travel spectrum. Both past and future oriented systems involve similar brain areas and show common deficits in amnesiac individuals (for review see Suddendorf & Corballis, 2007). Suddendorf and Corballis (1997) suggested that the reconstructive and experiential nature of episodic memory is also what allows humans to try out different future scenarios.

Inspired by Suddendorf and Corballis (1997), Tulving's subsequent (2002; 2005) definition of episodic memory has been modified even further to reduce the importance of spatial and temporal contexts. Now Tulving (2002; 2005) points to three aspects that distinguish episodic memory from semantic memory: the self, autonoetic awareness, and subjective time. These three features are intimately connected to each other and all center on the experiential component of episodic memory. These three concepts basically can be distilled into the idea that to have episodic memory there must exist an individual who is aware of themselves and has the ability to perceive of themselves as having a unique past, present, and future through which they can mentally travel.

Tulving's addition of autonoetic consciousness and other self-reflective components to the definition of episodic memory, however, has made episodic memory much more difficult to operationally define and test, particularly without the use of language. Perhaps because of the difficulty of defining and testing autonoetic consciousness, some subsequent researchers in human memory prefer to define episodic memory in terms that more closely resemble Tulving's original (1972) definition. For example, Baddeley (2002) notes that "The essence of this [episodic memory] is its specificity, its capacity to represent a specific event, and to locate it in time and space" (p. 3). Mayes and Roberts (2002) likewise emphasize that episodic memory is about representations and relationships. They argue that episodic memory is about the associations of information from perceptual and semantic sources and about the way that things are located in time and space in relation to each other as well as to the self (Mayes & Roberts, 2002).

From these definitions, we have attempted to create a general context and outline of the concept of episodic memory. Now we want to take a moment to consider what the picture of episodic memory should look like by seeing how humans display episodic memory.

Examining the Picture on the Box

Adult Humans

As the definitions of episodic memory have varied, so have the tests to assess it. Initially, much of the research into human episodic memory arose in case studies of brain damaged and amnesiac individuals. Amnesiac patients typically lack the ability to recall personal events from their past (*retrograde amnesia*) or lack the ability to form new personal memories (*anterograde amnesia*). Both retrograde and anterograde amnesia for personal events most often occur as the result of brain injury either from acute trauma or from a progressive neurodegenerative diseases that particularly affects the hippocampus and other medial temporal regions (for review of episodic memory deficits from neurodegenerative diseases see Deweer, Pillon, Pochon, & Dubois, 2001).

While the presence of amnesia typically indicates deficits in episodic memory, it does not imply that the deficits are *only* to episodic memory. Squire (1992) suggests that all of declarative memory, including both episodic and semantic memory, is impaired in amnesiacs. Vargha-Khadem et al. (1997), however, studied three children with focal hippocampal lesions who appeared to show impaired episodic memory but retained intact semantic memory. This finding led Tulving and Markowitsch (1998) to conclude that the hippocampus is necessary for episodic memory while semantic memory relies on the surrounding cortical structures but not the hippocampus itself.

Tulving has studied two amnesiac patients who appear to have lost their episodic memory abilities while maintaining their semantic memory. Both patients N.N. and K.C. apparently lost their autonoetic consciousness as the result of brain injury. N.N. had no episodic memory of events in his life. Although he could answer fact based information about his past and learn new information about the world, he had no feeling of re-experiencing or remembering any past event (Tulving, 1985b). Furthermore, he could not project himself into the future either; when asked what he would do tomorrow, N.N. reported that he did not know and that trying to imagine tomorrow was just total blankness in his mind. Tulving (1985b) notes that N.N. lost his ability to experience subjective time and was essentially living in a “permanent present” (p. 4).

Similarly, K.C. had no memory of any events in his life and when events were described to him, he had no recollection or even familiarity with the events having ever occurred (Tulving, 2005). Although K.C. has learned new semantic information such as completion of three word sentences, he cannot recall having learned the sentences or anything about the learning episode (Tulving, 2005). This seems to contrast with Tulving's (2005) claim that semantic information is all that is necessary for an individual to recall at time B events that occurred at time A. If semantic memory is all that is necessary, one would expect that K.C. could recall some information about episodes from his life or from laboratory visits even if he could not re-experience these events *per se*. For example, K.C. was asked about his brother's death and showed no recollection or familiarity of the event. At the very least, we would expect K.C. to recall what happened to his brother or perhaps the date when he died, given the significance of the event and Tulving's claim that semantic memory is capable of storing this information.[2]

Studies of other amnesiac patients, such as K.C., have shown similar deficits with impaired or absent abilities in mental time travel, but relatively preserved semantic memory of the past and future (for discussion of K.C.'s history see Tulving, 2002; 2005). Interestingly, these two brief descriptions of case studies of amnesiacs show that memories of past events and imagining future events were significantly impaired. However, more research is necessary to show the extent that events can be stored purely by semantic memory and which memories require episodic memory. Similarly, it is important to clearly establish that the impairments are uniquely episodic in nature and not the result of broader declarative deficits (for example see arguments in Squire, 1992).

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[2] However, it may be that K.C., contrary to Tulving's assertion, shows extensive retrograde amnesia for both episodic and semantic memories which may explain his deficits remembering such facts about his life (for review see Moscovitch et al., 2005).

In non-amnesiac populations, episodic memory has often been studied using memory of word lists, including recognition, cued recall, and free recall studies (e.g., see Tulving 1985b; Perfect, Mayes, Downes, & Van Eijk, 1996; Mather, Henkel, & Johnson, 1997; Yonelinas, 2001). Many of these tests can be completed not only by using episodic memory but also by semantic memory. Note, however, that this contrasts to Tulving's (1972) original view that most laboratory tests of memory, particularly word list memory, was the realm of episodic rather than semantic memory. In the cases of semantic recognition, the participant does not have to recollect the event of having studied the word but merely knows that the word was present on the list through some other mechanism such as how familiar the word seems (Gardiner, 1988; Tulving 1985b). Although word list studies are useful for their high degree of experimental control, they do not really resemble the every-day experiences of episodic recall.

Testing a more naturalistic style of episodic recall has been carried out by using narrative-structured recall of episodic memories. Kopelman, Wilson, and Baddeley (1989) designed a test to measure recall of events from different life periods (for a similar test see Borrini, Dall'Ora, Della Sala, Marinelli, & Spinnler, 1989). The test included questions asking the participant to report on experiences from different periods of their life. The answers to the questions were then scored based on the level of detail included as well as whether there were spatial and temporal contexts recalled. Kopelman et al. (1989) found a decrease in episodic memory based on the age of the memory in amnesiacs, with recent memories lost and old memories primarily intact[3]. All answers were checked with at least two family members and scored for accuracy. The test proved to be a valid and reliable measure of episodic memory. Many studies have subsequently used this method to assess the effects of brain damage on episodic memory recall (e.g., for review see Kopelman et al., 1989; see also Della Sala, Laiacona, Spinnler, & Trivelli, 1993).

In a long term study of episodic recall, Wagenaar (1986) examined his own episodic memory by looking at the contents of different event memories from a period of six years. More specifically he examined his ability to recall *what, when, where*, and *who* was involved in an event after being given one piece of information as a cue. Wagenaar (1986) found that *what* as a cue was the most successful at retrieving subsequent information about the event while *when* as a cue was the least successful. Furthermore, *when* was often completely missing from the recall of the event. Wagenaar suggests that temporal location "is stored [in episodic memory] in a very rough manner, or maybe not at all" (1986, p. 246).

Despite Wagenaar's (1986) findings of the relative difficulty of using *when* information to retrieve episodic memories and even the lack of *when* information for some events, many still argue that the *when* component in episodic memory is the key to human uniqueness in episodic memory (e.g., Suddendorf & Corballis, 1997; Tulving, 2002; Roberts, 2002). But clearly, *when* in a strict and specific sense is not required for

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[3] But, see Moscovitch et al. (2005) for evidence and arguments that episodic memory, particularly the rich, detailed re-experiencing of episodic memory, is completely lost for all memories in hippocampal amnesia while semantic memories may shows the typical temporal grading.

recall of an event. The way that humans time events is also relevant to understanding episodic memory. Adult humans' abilities to place an event in time typically involve one or more of three different strategies. The first is location-based time judgments, which involve locating the event in a temporal framework (e.g., that happened in March). Friedman (2005) notes that this method of timing is most closely linked to semantic representations. The second method of timing judges the distances in the past that events occurred (e.g., that happened years ago). The third timing method involves judging the relative order of events (e.g., that happened before my birthday). These different strategies are useful for different kinds of time placements of events. Distance-based time judgments seem to be more reliable for the timing of events that occurred in the past few months or for making quick and coarse judgments of timing when low levels of other context information are stored (Friedman 1993; 2005). Both long-term and short-term tests of memory for order of events have also been used in humans as evidence for episodic memory (see Healy, Cunningham, Shea, & Kole, 2007 and review Roberts, 2002). Although humans can order the occurrence of events, they are often quite poor at recall of the specific serial order in which they experienced events over a relatively short time period, such as events within an episode (Burt, Kemp, & Conway, 2008). Instead, serial order judgments appear to be most accurate when the events occurred farther apart or are meaningfully related in some way (Friedman, 1993).

The location-based time judgments involve the retrieval of information about time laid down at the time the event memory was encoded (Friedman, 1993). The most popular early view of location-based time judgments was the time-tagging approach. In this view, each episodic memory contains a time tag that is assumed to store a specific time of day and/or date with each memory encoding. Time tags may be used in the encoding of a small number of important events (e.g., September 11, 2001), but these are apparently rarely used in every day memory of events (Wagenaar, 1986; see also Friedman, 1993). Because the memories do not seem to contain time tags, any location based time judgments must rely on another approach.

In general, the evidence seems to favor a reconstructive approach to location-based timing of memories (see Friedman, 1993). Contextual aspects stored within the memory help us to place the occurrence of an event by using our knowledge of time patterns to make inferences about when an event likely occurred (Friedman, 1993). Reconstructive processes of timing are more accurate at placing an event into a temporal context and are better over longer time periods (periods longer than several months), but require more effort and greater contextual information within the memory to accurately judge the timing (Friedman, 1993; 2005). The reconstructive approach to timing suggests that the *when* component of episodic memory may not be intrinsic to the memory, but a re-creation from our semantic memory and information contained in episodic memories. The reconstructive theory of timing is the most important for mental time travel in humans because it is the only one that allows humans to consider *when* in the future an event is likely to occur because it allows for flexible recreation of time (Friedman, 2005).

Not just time, but likely much of episodic memory is the result of reconstructive processes. Research on episodic memory in humans has found that episodic memories are prone to errors due to suggestion and familiar scripts of events (Schacter, 1999). These false aspects of memories even activate many of the same neural networks as true memories (Okado & Stark, 2005). This suggests that much of the content and location of episodic memory may be the result of reconstruction from general knowledge (i.e., semantic memory) rather than the re-experiencing of the memory as it occurred (Ferbinteanu, Kennedy, & Shapiro, 2006). Because of this reconstructive process, Ferbinteanu et al. (2006) argue that both autonoetic consciousness and the experience of mental time travel are merely an illusionary feature of consciousness based in semantic memory and not a central feature of episodic memory. Instead, they argue that, due to this reconstructive nature, the cognitive components that make up episodic memories can be studied independently of the experimental report. There is some support in human literature for the idea that the *experience* of episodic memory is separate from the *content* of episodic memory. The pathology displayed in *déjà vu* may be one example. People who experience *déjà vu* have feelings as though they remember an event, but without actually having any true content to re-experience given that the event never occurred (Mayes & Roberts, 2002). This clearly contrasts with Tulving's (2002; 2005) view of episodic memory which emphasizes the essential role of autonoetic consciousness.

In fact, Tulving has suggested that the content of episodic memory may be established and stored entirely as semantic memory and that the experience is the predominant aspect of episodic memory (Tulving & Markowitsch, 1998). If this is the case though, then it is not clear why a separate memory system is necessary for this experiential “add-on”. Are the memories fundamentally different if it is only the manner in which they are recalled that changes? Furthermore, it seems that if this were true then the life events missing from the amnesiacs’ memories should be accessible through semantic memory even if they cannot be experienced—but they are not.

Developmental Perspectives

Experimental tests of children’s episodic memory, particularly the experiential components, like the study of animal episodic memory to be discussed, are complicated by the lack of language skills to express their memories and their autonoetic experiences. Also complicating the study of episodic memory in children is the phenomenon of childhood amnesia. Childhood amnesia refers to phenomenon of absence of most people’s memories of their life before the age of 3 or 4 (Loftus, 1993; Rubin, 1982; Usher & Neisser, 1993). One theory of the mid-childhood development of episodic memory attributes the slow development at least partially to the improvement of language skills in children. Several studies of children’s development of language abilities and narrative structure have found a relationship between the complexity and stability of the narrative and better episodic memory (for review see Fivush, Haden, & Reese, 1996; Pillemer, Picariello, & Pruett, 1994). But we know from amnesiac patients such as N.N. and K.C. that language, *per se*, is not sufficient to maintain episodic memory.

In contrast, others believe that language is not even necessary for episodic or autobiographical memory, but rather that language may merely play a role in the stability and accessibility of episodic memory (Sutton, 2002). The criticality of language or not in the development of episodic memory has clear implications for animal episodic memory. If language is a requirement for the production of episodic memories, then the search for episodic memory in animals is likely futile. If instead language supports but is not necessary for episodic memory, then the presence of animal episodic memory is a much greater possibility.

The existence of childhood amnesia and the lack of verbal skill to express episodic memory have led many developmental researchers to conclude that episodic memory develops relatively late, around the age of four, compared to other memory systems which typically develop in the first two years (Perner & Ruffman, 1995; Nelson, 1993).

Although laboratory studies of children's episodic memory point to poor or absent episodic recall in very young children, Gathercole (1998) points out that typically, laboratory studies of autobiographical memory are in contrast to the views of parents and child-care providers who report that children as young as 2 years can relate rich and complex narratives about past events. This may be attributable to the fact that most laboratory tests of episodic memory involve the passive observation and report of observed events that occurred rather than the direct involvement of the child in the event reported (Gathercole, 1998). The tests also depend on the child's understanding of the temporal words used in the questions (see also Suddendorf & Busby, 2005;

Friedman, 1993, 2005 for review of understanding of temporal words in children). Furthermore, children may lack the social narrative skills to convey their experiences when speaking with a stranger (Gathercole, 1998). Alternatively, parents may underestimate their own projective contribution to children's "recall" of events.

In attempts to remove the need for children to use language to express their memories and subjective experiences, non-verbal tests of episodic memory have been attempted. Non-verbal tests of episodic memory are important for determining whether the developmental differences in episodic memory are real or are an artifact of the testing procedure. The ability to devise tests and measure episodic memory in pre-lingual children has clear implications for the ability to find episodic memory in animals as well.

Tests of *elicited imitation* in pre-lingual children may provide support for the view that language is not a requirement of episodic memory. Children view a sequence of events, such as putting together a toy gong, and are then asked to recall the event sequence after a delay of hours, or up to a year later(see Bauer & Mandler, 1989; Meltzoff, 1988; Bauer, Hertsgaard, & Wewerka, 1995). These non-verbal tests of episodic memory have found that children as young as 13 months can recall after a delay of 6 weeks information seen only once (Meltzoff, 1988), and 2-year olds can recall the information after delays as long as 8 to 12 months (Bauer, Hertsgaard, & Dow, 1994). McCormack and Hoerl (1999) critiqued studies of deferred imitation as examples of episodic recall because the children only show that they recall the sequencing of events in generic terms of what happens and not that they remember the events within a relational and event specific temporal framework. This is another case where more studies of amnesiacs would be beneficial. If amnesiacs were incapable of completing elicited imitation tasks, it would be difficult to argue that the children are capable of completing the task without episodic memory. In fact, one study of amnesiacs has found that they are unable to accurately complete an age appropriate elicited imitation task (McDonough, Mandler, McKee, & Squire, 1995), but the study did not differentiate between individuals with deficits only to episodic memory and those with episodic and semantic deficits.

Tulving (2005) devised a non-verbal test of children's mental time travel abilities, which he proposed could also be modified for animal models. For his non-verbal test, Tulving (2005) is most interested in whether children can plan for the future rather than remember the past. His test is called the "Spoon Test." The idea behind the spoon test came from a children's story: a young girl dreams about going to a friend's birthday party where the guests are given chocolate pudding. Sadly, the little girl cannot have any pudding because everyone had to have her own spoon, and she has forgotten to bring a spoon. The next night, the girl is determined to not be disappointed and so she goes to sleep holding a spoon. Tulving (2005) notes that this little girl was showing the clear ability to mentally time travel into the future where she would need to have a spoon. Tulving (2005) suggests that any child or animal that can *plan* to bring with them something that is necessary for fulfilling future needs in another location will have passed the spoon test.

Based on the spoon test, Suddendorf and Busby (2005) tested children's ability to plan for future motivational states in a task they called "the rooms task." They had children enter a "boring" room in which there was only a puzzle board without puzzle pieces (experimental group) or an empty room (control group). They then took the children to a room that was full of toys and allowed them to play for several minutes. The children were then allowed to choose an item: puzzle pieces, a paint brush, crayons, or a coin to take back with them to the first room. The 4 and 5-year-olds in the experimental but not the control group chose to bring the puzzle pieces back into the boring room. The control group of children was equally likely to bring the other objects into the boring room. In contrast, the 3-year-olds showed equal, moderate-level preference for the puzzle pieces in both the experimental and control groups, indicating that there was no anticipation that the puzzle pieces would be the most appropriate to take into the boring room with the puzzle board. These findings imply that the development of time travel into the future occurs at around the age of 4.

Both the spoon test and the rooms task might provide ways of testing non-verbal animals for the ability to mentally time travel into the future. There are likely other useful tests as well.

Further complicating our understanding of children's episodic memory is our relative lack of knowledge about brain development. Little is known about the development in humans of neural structures involved in episodic memory. The typical ways of studying neural substrates in adult humans, such as PET and fMRI, are not practical for studying infants, which limits the imaging techniques to non-invasive techniques such as ERP that lose much of their spatial resolution, particularly for subcortical structures (Bauer, 2007). Finally, the problems of testing for episodic memory in infants and young children without verbal abilities to express memories in narrative form have further prevented the understanding of the development of neural structures involved in episodic memory. Most of the evidence about the development of neural structures has come from examining development of structures associated with human episodic memory in animal models (Bauer, 2007). With good tests of episodic memory in animal models, we could also improve our understanding of the developmental processes of episodic memory.

Animal models would also be beneficial in understanding the decline of episodic memory in old age. Episodic memory has been proposed to be one of the last memory systems to develop and one of the first memory systems to go in old age (Tulving, 2002). However, little is known about the causes and progression of episodic memory loss. Once again animal models of the decline in episodic memory due to aging could provide us with additional information about decline due to structural changes.

An animal model of episodic memory would be useful to test for the functional properties and determinants of episodic memory, to test for specific brain areas necessary for episodic memory, as well as to model age-related development and decline in episodic memory. One impediment to progress in the efforts to find effective treatments for neurodegenerative diseases involving episodic memory loss, such as Alzheimer’s disease, has been the lack of a good animal model in which to test new treatments (Dere, Kart-Teke, Huston, De Souza Silva, 2006). Making the task of finding an animal model more difficult has been the claim that animals lack the capabilities of possessing episodic memory (Tulving, 1983; Suddendorf & Corballis, 1997). As Dere et al. (2006) point out, the requirements for proving episodic memory in humans are relatively weak because people start with the assumption that because humans have the memory system, they must be using it. In contrast, the requirements for proving episodic memory in animals are quite stringent because it is assumed that they lack the ability.

Humans have a long history of claims of uniqueness in comparison to animals. Many of the attributes which were once thought to be only human, such as "self-recognition", tool use, and symbolic thought, and have subsequently been shown in other animal species (e.g., Gallup, 1983; Goodall, 1986; Greenfield & Savage-Rumbaugh, 1990). Episodic memory may just be another in the long line of abilities to be crossed off the list of those unique to humans.

In this section, we have tried to create a context and border into which we can place the pieces of animal episodic memory. It is clear from this brief review of definitions and human studies that there are still a few missing pieces and that the borders are not straight lines but rather are convoluted and ever-shifting edges. Our efforts now turn to assembling the rest of the puzzle of episodic memory in the animal mind. Just as the proposed definitions of episodic memory changed over time so has the research into episodic memory capacity in animals.

Sorting the Pieces: Do Animals Have What it Takes?

Before trying to assemble pieces, we want to make sure that the pieces are the same colors and that we have the pieces to the right puzzle. Namely, we want to review some of the evidence that suggests that animals have the potential to express episodic memory such as the functional and evolutionary potential for episodic memory as well as the neurobiological structures involved.

Function and Evolutionary Potential

For such a complicated and sophisticated memory system to develop, it seems likely that episodic memory must have some functional significance to necessitate its presence. Conway (2002) proposed that the functional value of episodic memory might be to take sensory-perceptual information and organize it into coherent chunks of experience that can be better processed and analyzed for more successful goal attainment. Episodic memories allow an actor to track their progress in completing a variety of tasks throughout the day by creating the feeling of having experienced the task rather than just imagining or planning the activity (Conway, 2002). However, patients with damage primarily to hippocampus cannot imagine new experiences (Hassabis, Kumaran, Vann, & Maguire, 2007). The attempts at creating an imagined experience in these amnesiac patients produced fragmentary images without a clear holistic representation of the event. This suggests that perhaps the same mechanisms occur for both experiencing the past and imagining new situations.

Sherry and Schacter (1987) proposed that the episodic memory system developed to allow organisms to use context to tag different experiences as important.

Episodic memory in animals could allow them to track the current state of different food sources within their environment such as food caches in scrub jays or ripe fruits in primate species (Schwartz & Evans, 2001). Ecologically, it makes sense for animals to track *where* and *when* relevant events happened to them such as finding food or a predator's attack (Gallistel, 1990; Wilkie, 1995). Because the world is a dangerous place with changing food patterns, it is beneficial for animals to be able to represent rich details of context of their experience of events that occur even only one time (Morris, 2001).

Additionally, episodic memory may also be important for tracking social relationships and standings within complex social groups (Schwartz & Evans, 2001). In support of the social role of episodic memory, humans with social deficits (e.g., autism) also tend to have deficits in episodic memory and vice versa (Klein, Chan, & Loftus, 1999). Traits and capabilities that have functional value for survival and reproduction are, of course, those that are selected for by evolution. Typically once a useful trait emerges, it and its physical substrate remains conserved within species and to subsequent species derived from that species especially when the same selective pressures on the species are maintained (see Reeve & Sherman, 1993).

Two families of animals, in particular, may be good places to search for episodic memory. Both apes and corvids have relatively large brains for their body size and large areas responsible for decision making and executive control (nidopallium for the corvids and prefrontal cortex for the apes; as reviewed in de Kort, Dickinson, & Clayton, 2005). Moreover, they are long lived with complex social structures (Emery &

Clayton, 2004). Many of the environmental demands on the apes and corvids are also similar. For example, both must search for perishable food across space and time and understand relationships of individuals within a social group (Emery & Clayton, 2004). Emery and Clayton (2004) have proposed that these demands have led to the evolution of complex cognition common to corvids and apes including: causal reasoning, flexibility, imagination, and prospection. This cognitive tool kit is closely related to some of the elements of episodic memory. While corvids and apes might be the best places to begin the search for episodic memory in animals, they are certainly not the only species that would benefit from such a memory system. Thus, the search should not be confined to these species.

By understanding the presence and distribution of different memory systems across humans and non-humans, we may come to better understand cognition more broadly as well as the bases for the evolution of specific cognitive capacities.

Neurobiology of Episodic Memory

The cognitive capacities for episodic memory across animal species are likely directly related to the development of critical brain structures involved in such cognition. Although there has been research into the areas of the brain that are involved in episodic memory, there is still very little known about the role of each brain area in the production of episodic memory. Imaging studies and evidence from patients with brain damage support the involvement of a large number of structures and networks involved in episodic encoding and retrieval, including medial temporal regions and prefrontal regions of the brain (Deweer et al., 2001).

In the medial temporal regions, the hippocampus was first implicated in episodic memory because of findings of amnesia in patients with hippocampal damage. Tulving (1993) and Vargha-Khadem et al. (1997) have proposed that episodic and semantic memory can be distinguished by their differential impairment following hippocampal damage. They suggest that when damage is limited to the hippocampus, only episodic memory is impaired, but when damage extends to a broader region of the medial temporal lobe and parahippocampal structures, both episodic and semantic memories are impaired (Vargha-Khadem et al., 1997). Although semantic memories can activate the hippocampus, they do not seem to rely on the hippocampus the way that episodic memories do (Moscovitch et al., 2006).

Because most of the human research on the neurobiology of episodic memory is based on naturally occurring brain damage to different areas, which is rarely if ever localized, it is difficult to determine from these important case studies which structures are uniquely involved in episodic memory and what the contributions of other damaged structures may be. It is impossible to say with precision in human patients that certain structures caused the episodic memory deficits because there are so many other factors that could be contributing to human episodic memory deficits. In fact, there is a great deal of argument over the structures necessary for episodic and for semantic memory (e.g., see Squire & Zola, 1998). An animal model of episodic memory would allow for more precise experimental lesioning and to control for extraneous individual differences to better understand the contribution of each structure.

Interestingly, most of the structures that are hypothesized to be essential for episodic memory have been well conserved across mammals and indeed much of the animal kingdom (e.g., Burwell, Witter, & Amaral, 1995). Morris (2001) notes of the neurobiology literature that "there are no obvious cellular, connectional or biochemical differences to which we might relate the supposed differences in conscious awareness of animals and humans" (p. 1459). The same conservation of structures appears to be true for episodic memory as well. The hippocampus contains both similar cell types and connections to other brain structures across a variety of mammalian species (Amaral & Witter, 1989). Additionally, there seem to be homologous structures to the hippocampus in birds (medial pallium), reptiles (medial cortex), and fish (lateral telencephalic pallium; for review of evolution see Northcut, 1981). In addition to structural similarities, further support for elements of episodic memory being present across phylum in the hippocampal homologues comes from the finding that, like in mammals, allocentric spatial learning is impaired following lesions to the medial cortex in reptiles and the telencephalic pallium in teleost fish (Rodriguez et al., 2002). Intriguingly, correlations between hippocampal formation size and spatial abilities have been found across birds and mammals (Krebs, 1990). The hippocampal structure is particularly large in bird species that store food in caches compared to non-storing species (Krebs, 1990); similar results exist in mammalian research on the spatial demands of voles (Sherry, Jacobs, & Gaulin, 1992). With the additional association of the hippocampus with episodic memory, it might be predicted that selection for episodic-like memory would further select for a larger hippocampal formation

(Pravosudov & de Kort, 2006). In fact, relative to other corvid species, the western scrub-jay has a large hippocampal formation, perhaps because of its need to track rates of perishable food caches (Pravosudov & de Kort, 2006).

Recent studies in humans (Ekstrom et al., 2003), primates (Wirth et al., 2003; Yanike, Wirth, & Suzuki, 2004), and rodents (Wood, Dudchenko, Eichenbaum, 1999) have implicated the hippocampus in two of the key components of episodic memory: integration of objects and events and temporal organization. Both spatial and non-spatial features of events are encoded in the hippocampus in conjunction with ongoing events (Eichenbaum & Fortin, 2005).

In humans, the frontal lobe has been implicated in the autonoetic and experiential components during retrieval of episodic memory. Frontal lobe damage results in both source amnesia (Schacter, Harbluk & McLachlan, 1984), and impairments in memory for *where* information was obtained, order (Shimamura, Janowsky, & Squire, 1990) and recency judgments of events (Milner, Corsi, & Leonard, 1991). Wheeler, Stuss, and Tulving (1997) suggest that all of these impairments are the result of the loss of autonoetic consciousness. Namely, people with frontal lobe damage are no longer able to mentally travel back to an event to retrieve contextual details about that event. This may suggest that the content information of episodic memory is predominantly hippocampally dependent while the experiential component in retrieval is dissociable from the content and is frontally dependent (or mediated).

In contrast to the relative conservation of the hippocampus across species, the prefrontal cortex does show considerable size and development differences when humans are compared to other mammals. The prefrontal cortex is typically much larger in adult humans than other mammals (Wheeler et al., 1997) and takes a long time to reach full maturity (Dahl & Spear, 2004). However, humans do not have the largest prefrontal cortex; rather, the spiny anteater takes first prize in proportional size (Divac, Holst, Nelson, & McKenzie, 1987). Thus, while the size of prefrontal cortex in comparison to most animals would suggest that this could be a structure that accounts for differences in episodic memory, under this logic the spiny anteater should show superior episodic memory.

The fact that many structures are well conserved does mean that an animal model could be useful for understanding human neurobiology of episodic memory, but of course, accurate tests for the many elements and features of animal episodic memory are required before animal models of neurobiology can be used effectively.

From a functional, evolutionary, and neurobiological standpoint, there is no obvious reason that animals should not have the capacity to represent events in rich contextual detail, like those found in episodic memory.

Laying Down the Pieces for Episodic Memory

With our pieces sorted, we see that animals have the neuroanatomical structures necessary for episodic memory as well as many of the evolutionary pressures that likely led to the development of episodic memory in humans. Now that only leaves the assembly of the pieces into our puzzle.

Tulving's emphasis on autonoetic consciousness in the definition of episodic memory makes measuring episodic memory objectively in humans—let alone animals— a most difficult undertaking! This is particularly true in non-human animals and pre-lingual children because it is difficult if not impossible without the use of language to report on the subjective nature of the experiences of the past.

There is some hope of finding ways of measuring subjective experience in animals. It was once thought impossible for animals to report on any subjective experiences, but there is some evidence that animals can introspect. Lubinski and Thompson (1987; see also review in 1993) found that pigeons could report on their internal states and even "communicate" them to another pigeon. Pigeons were trained to peck choice keys in response to the "sample stimulus" of their drug-induced state. The pigeons received cocaine, pentobarbital, or a saline injection and then were given three choice keys. The pigeons quickly learned to report on their internal states and were able to generalize this learning to novel but related drugs (e.g., Chloradiazepoxide for pentobarbital and d-amphetamine for cocaine; Lubinski & Thompson; 1987). Lubinski and Thompson (1993) also established a communicative exchange in which one pigeon pecked a key to ask a pigeon in a separate chamber "How they were feeling." The pigeon in the second chamber had to respond by pecking the key that corresponded to their drug-induced state. From this the initial "asking" pigeon had to examine the "drug" key that the other pigeon pecked and peck the key that corresponded to that class of drugs in order for both pigeons to be fed. Likewise, Cowey and Stoerig (1997) showed that monkeys with lesions to the striate cortex could report their subjective experience of blindsight, the inability to see a portion of the visual field, even though they could accurately reach toward the object.

Given that it may be possible to someday measure more subjective states, there is some hope of finding autonoetic consciousness in non-human animals. This is hampered, however, by the lack of clear non-verbal behavioral criteria for identifying autonoetic consciousness. Even in humans, it is far from clear when an individual is experiencing autonoetic consciousness aside from asking them if they remember and are re-experiencing a past event. Even without a current way to measure autonoetic consciousness in animals, the quest to find episodic memory in animals is not lost. After all, the experiential component is only one property of episodic memory—and it may be epi-phenomenal. Moreover, we cannot expect that all animals experience things in the same way as humans[4]. We do not expect a dolphin or an eagle to experience the visual world in the same way as each other or as humans do, so it makes sense that the experiential aspects of other systems would also be different across species. Thus, animals may have the content of episodic memory but experience it in a species specific way (Ferbinteanu et al., 2006). The differential experience of recollection also does not mean that the same psychological and neurobiological mechanisms of episodic memory are not present across species and accomplish the same functions but with different experiences (Ferbinteanu et al., 2006).

In recognition of our current inabilities to directly measure autonoetic consciousness in non-lingual species, many researchers (e.g., Clayton & Dickinson,

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[4] For in fact, all humans do not perceive or experience identical objects in the same way due to cultural differences (e.g., Davies, Sowden, Jerrett, Jerrett, & Corbett, 1998).

1998; Zentall, Clement, Bhatt, & Allen, 2001) have instead adopted the term "*episodic-like"* memory to recognize the fact that animals may exhibit features of episodic memory even if the experiments cannot show that the animals experience autonoetic consciousness.

In attempting to find episodic memory in animals, researchers have broken episodic memory into its elements, features and properties. Clayton and Dickinson (1998) decided to examine the elements of episodic memory identified by Tulving (1972). Clayton and Dickinson (1998) specified that an event or episode has three distinct features: *what* occurred or was involved in the event, *where* the event occurred, and *when* the event occurred (i.e., the context dependent nature of episodic memory). They therefore looked for animals' abilities to use information about what happened, the spatial locations of an event, and the time of an event, which, as aforementioned, they termed "episodic-like" memory (Clayton & Dickinson, 1998). Many events can share content and location, but each event is unique in time. Thus, they claim that the element of *when* of an event is essential in forming a unique episodic memory code. Clayton et al (2003) claim this requires that any test of episodic memory must be for a memory formed, typically, in a single exposure, rather than the result of repeated exposures. As similar episodes are repeated, people tend to develop general knowledge and script-like recall of events rather than a detailed memory of the specific occasions (Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006). While repetition of experiences certainly can produce semantic memories, repeated experiences do not necessarily preclude an episodic memory (e.g., see arguments in Moscovitch et al., 2005). For example, a person may have many kisses in their life and know generally how kisses go, but that does not mean that they do not also have an episodic memory of their first kiss that they can look back on. With animals, the inability to use language to give instructions often necessitates the repetition of situations and trials to teach the animal how to "play the game" and how to communicate what they know to us.

Each element, *what, where,* and *when,* of Clayton and Dickinson's (1998) episodic-like memory has been tested in animals. Research has long shown that animals can distinguish between different events and stimuli (e.g., von Fersen & Delius, 1989; D'Amato & Colombo, 1985; Williams, Butler, & Overmier, 1990; Tinklepaugh, 1928, 1932) which indicates knowledge of *what* occurs or *what* the outcome is. Animals also have a good representation of *where* things occur which has been the basis for many tests of animal memory over the last century (e.g., Small, 1901; Olton, 1979; Vander Wall, 1982). Finally, animals have been shown to understand *when* events occur relative to other events. Wilkie and colleagues have found that many species of birds can show the ability to track both *when* and *where* feeding occurs (e.g., pigeons in Saksida & Wilkie, 1994; for wild birds' abilities to use time and location information see Wilkie, 1995). Rats, on the other hand, track *when* and *where* food is available primarily under high stress situations such as during high response cost tasks (Widman, Gordon, & Timberlake, 2000), high numbers of lever responses (Carr & Wilkie, 1999; Carr, Tan, & Wilkie, 1999), or under extreme deprivation (60% of their free feeding weight) conditions (Lukayanov, Pereira, Mesquita, & Andrade, 2002). Animals also have the ability to time durations of events as well as the durations since an event (for short interval timing see Roberts, 1981; for longer intervals see Crystal, 2006).

Episodic-like Memory: Remembering What, Where, and When

Based on evidence of animals' abilities to show *what, where,* and *when* independently, we have established that all the building blocks exist for an episodic memory containing spatio-temporal contexts seem to be present in animals. Now we turn to how they can be combined to form a single episode.

Using differential outcomes, a procedure in which different food outcomes are used for each response, Thorpe and Wilkie (2007) found that rats were capable of remembering information about what food amount was available *where* and *when*. However, the researchers trained the animals on this task repeatedly. In other words, because there was no single event to remember, the task could possibly be remembered by a series of semantic rules. However, understanding animals' ability to time events using semantic memory is important given the likelihood that placing episodic memories in time relies heavily on using semantic memory given that much of human placement of events in time is based on semantic memory and the use of semantic memories may not exclude the presence of episodic memories (see above).

Episodic-like memory was the term coined by Clayton and Dickinson (1998) to refer to the recollection of *what, where,* and *when* a specific past event occurred, but perhaps without the autonoetic consciousness that is required of full-fledged episodic memory as defined by Tulving. This combination of elements in a single event memory has been tested in several bird and mammalian species.

Birds. Pigeons have been tested on their ability to report *what, where,* and *when*. Skov-Rackette, Miller, and Shettleworth (2006) had pigeons report on one of the three features of a stimulus that they saw. The pigeons were shown one of two shapes in one of eight locations, with either a 2 second or 6 second delay between presentation and testing. The pigeons were then asked to report either *what* the stimulus was, *where* the stimulus was located, or *how long ago* the stimulus was presented. The pigeons were able to answer any one of the *what*, *where*, or *when* questions with 80% accuracy, suggesting that all three features were encoded. However, Skov-Rackette et al. (2006) noted a lack of correlation between accuracy on the first question and accuracy on subsequent questions about the same stimulus, and they argue that this indicates that the features were represented independently rather than in a single bound memory.

The first successful attempt to show that animals can act on memories for distinct events and objects in time and space was done in scrub jays—a species that naturally caches food for later consumption. Clayton and Dickinson (1998) taught the jays that their preferred food of wax worms degraded after a long delay (124 hours) but remained fresh after a short delay (4 hours) while the less preferred peanuts never degraded. The jays showed a reversal of items they searched for during cache recovery, choosing wax worms if the interval since caching was short and choosing peanuts following long intervals. This demonstrated that scrub jays remember the specific content (*what*), the location of a cache site (*where*), as well as the length of time since the cache was made (*when*).

Because of the importance of this demonstration, several additional follow-up experiments tested for alternatives to explanations in terms of episodic-like memory. It was possible in that first experiment that the jays were not using a true integration of *when* events occurred, but rather judged the relative familiarity of the tray and chose worms when the tray was familiar and peanuts when the tray was relatively unfamiliar. However, in subsequent experiments, Clayton and Dickinson (1999c) showed the same pattern of behavior in the scrub jays even when the trays were made equally familiar for both food items (see also Clayton, Yu, & Dickinson, 2001 for a similar replication). Although this excludes familiarity based on the cache location, it does not exclude familiarity of the cache foods themselves. The jays could have learned to search for worms only when worms were familiar and the peanuts when they were familiar; thus, the jays could have been showing a recency effect rather than remembering an episode of caching.

Another criticism has been that the jays could have used a mechanism of passive or directed forgetting, in which they merely failed to retrieve the location of the wax worms, to guide their cache recovery behavior (de Kort et al., 2005). If the basis for choosing was passive forgetting, we would expect that forgetting would not be specific only to time but should generalize to a decrease in accuracy of spatial locations of all the cached food items. Control group birds did not experience degradation of wax worms (Clayton & Dickinson, 1998; 1999c). Under the passive forgetting hypothesis, the control group birds should have seen some decrease in accuracy of recovering the worms after 5 days. The control jays were highly accurate at recovering both wax worms and peanuts despite delays.

The mechanisms of directed forgetting may have allowed the birds to forget about worm locations more rapidly following experience with degraded worms. However, de Kort et al. (2005) showed that the jays could not be using directed forgetting to track the food to recover. They tested two groups of birds; one group was the standard *degrade* group that experienced degradation of wax worms following long intervals, and the other group, termed the *ripen* group, experienced degradation of the wax worms following short intervals but a fresh worm after long intervals. As seen in figure 1, the birds in the degrade group preferentially chose wax worms only after the short interval while those in the ripen group preferentially chose wax worms only after the long interval (de Kort et al., 2005).

The possibility still remains that the jays use a differential trace strength of *what-where* information from caching to make judgments about the current condition of food (Clayton et al., 2001), but Friedman (1993) has suggested that differential trace strength may be the way that humans record time in episodic memory. Furthermore, a trace strength explanation would predict that as retention times increase the ability to discriminate between caching episodes would decrease. The scrub jays showed differential searching even after retention intervals were lengthened to 172 hours (Clayton & Dickinson, 1999a).

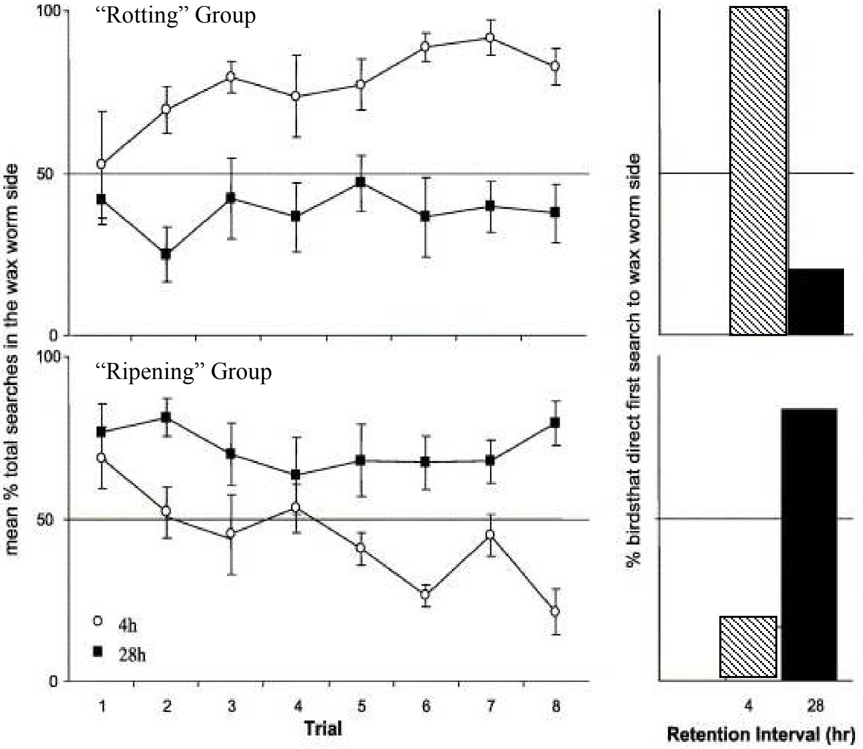

Figure 1. Experimental results from de Kort et al. (2005). The degrade group preferentially searched for worms only after 4 hours while the ripen group searched for worms only after 28 hours (figure re-created from de Kort et al., 2005).

It is quite possible that the processes of scrub jay cache recovery are mediated by both semantic and episodic memories. The jays must learn that decay of worms follows a rule based on time which is likely mediated by a semantic memory, but they then use that rule by applying it to the memory of a unique caching event fixed in time which seems to be mediated by episodic memory (Clayton et al., 2001). Because of our inability to give verbal directions to animals, testing truly trial unique events is quite difficult. Typically it is necessary to teach the animals how to "play the game" before we can test their memories. In some sense, humans also do this with children through continuous talk about memories and joint recall of events.

Following, Clayton and Dickinson's (1998) success with scrub jays, other researchers have tried to find evidence of episodic memory and episodic-like memory in a variety of other species.

In a test of another caching species, Zinkivskay, Nazir, and Smulders (2009) used large open caching trays to test the memory of magpies. Zinkivskay et al. taught the magpies to cache two different colored egg pellets. Once the birds were caching and recovering the pellets, they began replacing one color of pellets with beads following a short retention interval and the other color after a long retention interval. The birds had to learn to search only for the color of food that was "good" at the time. The birds did in fact show a change in the locations that they searched based on the length of the interval.

Rodents. Birds are not the only species to show elements of episodic memory. Tests of rodents have met with mixed success, but have used a variety of techniques to show a range of memory abilities.

Fortin, Agster, and Eichenbaum (2002) had rats judge the order of presentations of odors rather than estimating the passage of time since an event. They argued that the important component in human episodic memory is really the ordering of the occurrences of events[5]. The rats were given 5 odors presented sequentially, and, then, were given probe trials of two odors in which the rats were only reinforced for selecting the odor that had occurred earlier in the initial sequence of odors. The rats successfully chose correctly based on the initial order of the odors, but showed better performance as the temporal distance between the two items (number of intervening odors) increased. Because the rats were successful (about 75%) on comparisons of the order of middle odors in the sequence, it is likely that the rats represented the entire sequence of the list rather than relying only on primacy or recency.

When some of the rats were given hippocampal lesions, which selectively impair episodic memory in humans (see above), the rats' performance declined to near chance levels for all order judgments (Fortin et al., 2002). In contrast, the rats with hippocampal lesions were still as successful as normals at identifying odors that were not presented in the sequence. This indicates that the rats with hippocampal lesions were able to make judgments based on familiarity, but that familiarity was insufficient to judge the order of events. Eichenbaum and Fortin (2005) propose that the inability of rats with hippocampal lesions to make order judgments based on familiarity suggests that normal rats were using recall of the entire unique odor sequence to make their judgments.

Eacott, Easton, and Zinkivskay (2005) also looked for episodic-like memory in rats. Instead of the *when* used by Clayton and Dickinson (1998) or the sequential order used by Eichenbaum (Fortin et al., 2002; Ergorul & Eichenbaum, 2004), they used

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[5] Both long-term and short-term tests of memory for order of events have also been used in humans as evidence for episodic memory (see Healy, Cunningham, Shea, & Kole, 2007 and Roberts, 2002).

which context an event occurred in. Eacott et al. (2005) argue that both *when* and *which* are occasion setters that define unique experiences. Consistent with this notion, Wagenaar (1986) noted that often the general context of an event helps humans to localize time; for example, seeing DaVinci's Last Supper places the event in the occasion of "my trip to Italy" that can then be localized in time, "I went to Italy two years ago" (Wagenaar, 1986).

Eacott et al. (2005) taught rats that two objects reversed location based on *which* context: black maze vs. wire mesh maze. The rats were encouraged to seek out one of the two objects by habituating them to the other object in their home cage prior to the test; rats' preference for novelty meant that the rats routinely sought out the non-habituated object in the maze. For the rats to find the non-habituated "correct" object, they had to remember the conditional location of the object based on the context the rat was currently in and what object they had been exposed to most recently in their home cages. For example, if in the black maze, the novel object might be located to the left of the start arm; while if in the wire mesh maze, the novel object would be on the right side. The rats went to the location that contained the non-habituated object significantly more than expected by chance, about 2/3 of the time, thus showing *what-where-which context* in an integrated memory for the habituation episode. Although this experiment shows that rats can remember objects and the contextual information about the location of objects, it does not directly involve the element of time, which may be inferred from context in humans, but is not inferred specifically in this experiment and is certainly not directly measured. Many have argued time is the key feature that distinguishes episodic memory from other types of memory (e.g., Clayton, Griffiths, Emery, & Dickinson, 2001; Tulving, 2005) while others concur with Eacott et al. (2005) that time is not as important and may be recalled even in humans as an occasion rather than a temporally specific event (Suddendorf & Corballis, 2007; Friedman, 2007).

In an experiment closer to the set-up of Clayton and Dickinson (1998, 1999c), Bird, Roberts, Abroms, Kit, and Crupi (2003) tested whether rats could incorporate *what, where*, and *when*. Bird et al. (2003) forced rats to cache foods in different arms of a radial arm maze[6]. The rats cached either cheese or pretzels on each arm. The rats were then taught that when they returned to the maze after either a short or long delay (half the rats on each), the cheese had been degraded with quinine. The rats never learned to choose the pretzel arms over the degraded cheese arms. In fact, they showed a slightly greater preference for the cheese arms even after they were degraded! However, there may be several problems with this failure to show memory for *what-where-when*. One problem was that the rats experienced a general lack of motivation to search for food following experiences with degraded food items (as discussed in Bird et al., 2003); the rats in the degrade experiment did not have a strong tendency to return to arms of the maze on which they had cached food and instead chose “non-cache arms” almost as frequently as cache arms. This may be related to the fact that Norway rats do not show much caching behavior in the wild and what food is stored is usually stored in a single larder (e.g., Takahashi & Lore, 1980).

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[6] The forced cache procedure was completed by first teaching each rat to carry food from the arm entrance to a covered goal box. Once the rats had learned how to cache, they were forced to place food in each arm by blocking the entrance to arms that already had food cached in them.

More promising results were obtained by Babb and Crystal (2005; 2006). They also employed a radial arm maze to test for episodic memory of differential food replenishment rates. The rats searched a radial arm maze for food pellets and chocolate. Two sessions occurred per day; between sessions either a short (30 minute) or long (4 hour) retention interval was used. Four arms were available in the first session with one arm containing chocolate chips and the other three containing food pellets. During the second session, all eight arms were available and the food pellets were available only in arms that had not contained pellets or chocolate in the first session of the day, while the chocolate was only replenished if a long retention interval occurred between the sessions (Babb & Crystal, 2005; 2006). The rats learned to check the chocolate arm in their first four arm visits during long retention intervals, but they did not check the chocolate arm following short retention intervals. The rats appeared to have learned to revisit the arms that contained their preferred food of chocolate based on the differential replenishment rates.

In a replication and extension of Babb and Crystal (2005; 2006), Naqshbandi, Feeney, McKenzie, & Roberts (2007) also tested different groups of rats on memory for replenishment following either short or long intervals. As in the experiment by Babb and Crystal (2005; 2006), Naqshbandi et al.'s (2007) rats in the long delay replenishment group learned to return to the chocolate arm following long intervals but not to return following short intervals. Additionally, their short replenish group learned to return to the chocolate arm following short intervals but not to return following long intervals (Naqshbandi et al., 2007). Naqshbandi et al. (2007) also replicated these results using another food type (cheese), and rather than replenishing the food, they degraded the food with quinine based on retention interval. As in the case of replenishment, the rats learned to only visit the cheese arm when it was not degraded. It is not clear why this experimental configuration was successful where the Bird et al. (2003) experiment failed; nonetheless, it appears that rats, like some birds, can remember *what, where, when* in an integrated memory.

Dere and colleagues (2005a; 2005b; 2006) propose that it is not sufficient to use trial unique events (as was done in all of the previous experiments) because they could produce rule based learning such as “if it has been a long time since I was in this context, go for chocolate.” Instead they suggest that completely novel events be used to establish episodic memory. To do so, Dere, Huston, and De Souza Silva (2005a) had mice recall the location (*where*) of recent and old (*when*) novel objects (*what*) in a novelty preference task. The mice were given two trials and a test session. In the first trial, the mice were shown four identical objects (e.g., spheres) and allowed to explore them for 5 minutes. The mice were then removed for 50 minutes and then given a second trial. The second trial involved four identical new objects (e.g., pyramids) in four new locations, which the mice were allowed to explore for 5 minutes and given another 50 minute break. Finally, for the test trial, the mice were presented with objects from the first trial, two old objects, one of which remained in its original position and one which was displaced from its original location. They were also presented two of the more recent objects (from trial two) that were in their original position (for a basic set-up see Figure 2). The mice showed an exploratory preference for first presented objects; this showed that they could discriminate between “old” and “more recent” objects (*what-when* discrimination). Furthermore, the mice showed a preference for the displaced “old” object in comparison to the unmoved “old” object; this indicates the mice also made a *what-where* discrimination because the mice recognized that the “old” object (*what*) was located in a novel location (*where*) (Dere et al., 2005a).

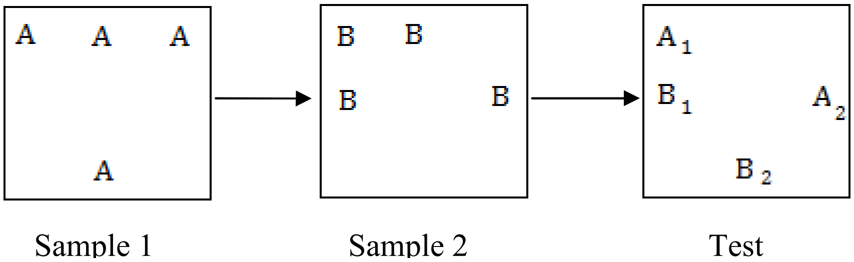

Figure 2. The experimental set up for Kart-Teke et al. (2006) study of *what-where-when* learning in rats. Sample 1 shows the placements of “old familiar” objects labeled “A” while Sample 2 shows the placement of “recent familiar” objects labeled “B”. Each set of objects was presented for 5 minutes with 50 minute inter-trial intervals. The test involved both old and recent objects in either their original, denoted by a 1, or a displaced (new) location, denoted by a 2. (Figure recreated from Kart-Teke et al. 2006).

This test was later repeated in rats, but with the addition of a displaced recent object (see Figure 2; Kart-Teke, Souza Silva, Huston, & Dere, 2006). The rats, in contrast to the mice, showed the greatest preference for the recent displaced object (B2 in figure 2) followed by the old unmoved object (A1 in figure 2). The fact that the rats preferred the old unmoved object (A1 in figure 2) to the old displaced object (A2 in figure 2) is somewhat surprising given that the displaced old object should be more novel than the stationary old object. The finding was replicated in two naïve groups of rats (see Kart-Teke et al., 2006 experiments 2 and 3). Kart-Teke et al. (2006) argue that the interaction between displacement and recency of encounter argue for an integration of *what-when-where* because the rats could not have responded in this way with independent retrieval of the temporal and spatial information, but they provide no analysis as to why the old stationary object was more preferred than the old displaced object.

One of the benefits of this novelty preference paradigm is that novelty preference has been studied extensively in rats and mice. The neurobiology of many aspects of novelty preference is well-understood (Dere et al., 2005a). Additionally, the paradigm involves unique experiences. Only two unique sample trials and one unique test trial is given to any rat, and the "question" of which object-location is most novel is therefore unexpected; this it is argued more closely mimics the spontaneous recall of episodic memory in humans (Dere et al., 2005a). Additionally, it could easily be repeated with various sets of novel stimuli which would be similar to giving human participants a new word list to study.

As with all relative familiarity tasks, it is possible that the *when* discrimination in this paradigm is the result of differential memory trace strengths for the different objects. Dere et al. (2005a) suggest that it is unlikely that there would be sufficient differences in memory trace strength between objects encountered 50 minutes apart to account for the findings[7]; preliminary findings from their lab did suggest that shortening the ITI to 30 or 20 minutes, does not affect the ability to judge the recency of the object presentation.

In another single exposure task, meadow voles were tested on their ability to track *what, where,* and *when* of mating status (Ferkin, Combs, delBarco-Trillo, Pierce, & Franklin, 2008). Meadow voles become most receptive to mating for a short period, 8-12 hours, after giving birth (post-partum estrous- PPE), so males who approach females during PPE are more successful at mating and producing offspring. Male meadow voles have overlapping home ranges that often contain many females in varying reproductive states. Thus, to take advantage of PPE, a male meadow vole must recall *where* females of varying reproductive states (*what*) are located and *when* the male last encountered the female in that state. Ferkin et al. (2008) tested these abilities in a laboratory setting, in which males were allowed to explore two chambers attached to a t-shaped apparatus where two females had been placed. The females were in various reproductive states including currently PPE, 1 day pre-partum, and not currently pregnant or lactating (control). After exploring the housing, the male voles were removed and later returned to a clean apparatus (all scents removed) either 30 minutes or 24 hours later. If the delay were 30 minutes, males preferred to return to the side where the PPE female had been located over the 1 day pre-partum and control females. If, however, 24 hours had passed, the male vole switched his preference to the side

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[7] It is not clear why Dere et al. (2005a) believe that 50 minutes is unreasonable length of time for the animals to make a discrimination when animals are capable of discriminating the recency of much shorter stimulus intervals (e.g., Grant & Roberts, 1973).

where he had encountered the female vole that had previously been 1-day pre-partum and would now be in PPE. The male showed no difference in preference for the formerly PPE female and control female 24 hours later. Thus, the male voles were able to track the *what, where,* and *when* of female reproductive states after a single exposure to those females. Most impressively, the voles appear to be able to track the *when* without using relative familiarity. Because the male voles had encountered both females at the same time, he could not be using familiarity to judge which vole would now be PPE. In some ways, this experiment could represent either mental time travel into the future or into the past. The male vole could either at the time of revisit travel back to recall the states of the female voles or he could plan to visit those females at a future time. This experiment has some very nice features that make it even more convincingly episodic-like memory than other demonstrations. For example, it uses one-trial learning of events which is commonly seen in human episodic memory, the argument for familiarity mechanisms driving the choice is not strong, and the value of tracking the status of mates sexual receptivity has biological functionality; voles that had the capacity to do so would have an evolutionary selective advantage. Additionally, we suspect that this program could be applied to other species as well.

Primates. If any class of animals might be expected to show episodic memory, it would be primates, as our nearest relatives. Work on episodic memory in primates, like the work in other species, has met with mixed success. Many tests of episodic-like memory have only looked at *what* and *where* aspects of episodic memory or have added a new component of *who* was involved with the event. The *who* component of events may be particularly important for many primates whose social groups are fairly dynamic (Schwartz & Evans, 2001). In fact, recall that in humans, Wagenaar (1986) found that the *who* component of episodic memory was remembered by humans more easily than the *when* component.

In a test with methods similar to those used in other species, Hampton, Hampstead, and Murray (2005) tested Rhesus monkeys for *what*, *where*, and *when* learning. The monkeys searched only the two locations where food had been available, rarely searching the unbaited location. The monkeys did show an effect of the length of the interval with long delays decreasing the preference for the degraded food on average, but still showing a high percentage of first searches to the degraded food site (over 60%). However, the preference difference following long and short delays was small and did not increase over time, as would be expected if the monkeys were learning the *what-where-when* connection. They concluded that Rhesus monkeys were unable to learn to temporally track the degradation of a preferred food source that degraded following long intervals. In fact, the tendency to search the degraded site actually increased slightly over the 30 test sessions. There are several problems with this experiment. The monkeys were required to locate both food locations on each trial before they were removed from the maze. Therefore, it was not a matter of whether they visited the degraded sites but rather a matter of the order in which they visited the degraded site. During training, the monkeys received 8-12 learning runs per day in which they visited both baited food sites. The same open field maze with three locations was used for each run in a given day and the monkeys all experienced searching for food at each location several times. During test trials, the animals experienced 8 runs in which they searched both food sites and then for the test trial they searched after a short interval (1 hour) and a long interval (25 hours) in each test session. Thus, the monkeys were supposed to learn that during the eight initial runs of the day as well as following a one hour delay the food replenished but that at 25 hours after the initial runs the food no longer replenished; the monkeys were then returned to start a new series with replenishing foods the following day. It is not surprising that the monkeys treated all of the locations as replenishing because the food was in fact replenished during all the training runs and was replenished every other day. In fact, compared to replenishment they rarely experienced the food degrading.

In perhaps the earliest ever test of episodic memory, Chimpanzees were tested on their ability to remember *what* and *where* information based on single-trial events. Tinklepaugh (1932) tested two chimpanzees on their ability to recall the location that a particular food was placed. He hid foods of differing value (bananas versus lettuce) in one of two containers while the chimpanzees watched. The chimpanzees were then given a retention interval of up to 72 hours during which time Tinklepaugh sometimes substituted different foods for the ones hidden in the containers. Both chimpanzees were described as showing surprise—even disgust— when the lettuce was found where a banana had been hidden, which Tinklepaugh argued indicated that the chimpanzees could remember both *what* food and *where* it was previously hidden. The judgment of surprise, however, was a subjective report on the part of Tinklepaugh.

Similarly, Menzel (1999) found that a language trained chimpanzee, Panzee, could remember *what* and *where* food had been hidden in her enclosure following a delay of up to 16 hours (for a further discussion of Panzee see spontaneous recall below).

Savage-Rumbaugh (as described in Schwartz and Evans, 2001) tested bonobos' ability to recognize *what, where,* and *who* information. The bonobo observed a research assistant carry an item to a specific location. Following a delay of 24 hours, the bonobo was asked who did the carrying by having her select the research assistant from a group of photos. She was then asked to use her lexical keyboard to indicate information about *where* and *what* objects were taken. There were only a small number of trials given to the bonobo, and she was correct on six of the eight questions posed to her. This gives some indication that Bonobos may recognize the components of past events, but more testing is necessary before the conclusion is confirmed.

Schwartz, Colon, Sanchez, Rodriguez, and Evans (2002) found that a gorilla, King, could indicate through the use of symbolic cards *who* previously gave him food as well as *what* food was previously given to him 24 hours before. They found a positive correlation between correct answers on *who* and *what* questions which they suggest indicate that the gorilla had a bound representation of the past event. Furthermore, King had been fed several food types during the 24 hour retention interval which required King to remember the specific episode of a specific experimenter giving him food rather than the use of familiarity of the food objects. Schwartz et al. (2002) inferred that this indicated that King had to also remember *when* the event occurred, although the basis of this inference is not obvious. King was also able to indicate the *order* and type of foods given to him up to 23 minutes after the presentation of the foods (Schwartz et al., 2005). To demonstrate this, King was given three food types, in a random order, and allowed to eat them. He was then asked what he ate, to which he always responded to by choosing one of five food cards in reverse order of the foods given (i.e., with the most recent food listed first). King's performance was most accurate for the most recent item (90%), then to the first food presented (60%), with the middle food item reported the least well, but above chance, recognition (50%). It seems that King's order learning may represent primacy and recency effects within the feeding event. However, this is a similar pattern to results in human memory studies of orders of naturalistic events (Burt, Kemp, & Conway, 2008).

From scrub jays to chimpanzees, the evidence is beginning to mount that animals have the capacity to learn what events occur in a particular location at a particular time. Although this evidence is impressive and important, there are still other aspects of human episodic memory that are not demonstrated by these *what-where-when* elements alone.

Looking for the Missing Pieces

The studies of episodic-like memory through examining *what, where,* and *when* have provided an excellent start on our puzzle, and they have established that some animals possess some of the content elements of episodic memory (See Table 1). But other features and properties have been ascribed to episodic memory suggesting that there are more pieces to the puzzle. In this section we are lifting up the couch cushions and checking under the rug for all of the remaining pieces-- the features and properties that we would look for in human episodic memory.

Structure and Flexibility

Just as Tulving seems to be constantly "updating" his concept of episodic memory in humans, so too do some animal researchers suggest updates for episodic-like memory in animals. Clayton and Dickinson have expanded on their initial research into episodic memory to include the *structural* requirements for the contents of episodic memory to be bound into a single memory and *flexibility* in the use of the episodic memory for guiding behavior (Clayton, Yu, & Dickinson, 2001; Clayton, Bussey, & Dickinson, 2003; see also review in de Kort et al., 2005). The *structure* refers to the fact that, in human episodic memory, the content elements of the memory are supposedly represented as a single coherent event rather than a series of separate facts. However, it is not clear if binding and flexibility are byproducts of episodic memory or are necessary features respectively of episodic memory.

The *flexibility* of episodic memory certainly contrasts to the implied inflexible nature of *implicit* or *procedural* memory (see discussion in Cohen, Poldrack, & Eichenbaum, 1997). In implicit memory, information is often gained slowly over time and typically is fixed in its behavioral deployment. For example, when a person learns to ride a bike, their implicit memory allows them to remember the body movements required to keep balance. Knowledge from episodic memory, and in fact semantic memory as well, can be used in a variety of other situations. Thus while flexibility seems to be a common feature of episodic memory it does not guarantee that the memory is not semantic in nature (see Tulving & Markowitsch, 1998).

The element of *structure* looks for the representation of the memory's content to be integrated into a form that makes each episode unique[8]. Clayton, Yu, and Dickinson (2001) tested the integration of *what, where,* and *when* information by confounding the content of two episodes. They had jays cache both worms and peanuts at different times in two distinct trays, such that upon recovery, the worms in the first tray would be degraded, but the worms cached in the second tray would be fresh. The jays differentially searched the two different trays, seeking out the peanuts in the first and the worms in the second, indicating that they had unique memories for each of the worm caching episodes. Because the items cached (*what*) in each tray were identical, the jays had to rely on a cueing of tray color (the *where*) that was bound with *what* and *when* information. This binding of the elements within each episode was termed by Clayton et al. (2001) as *what-where-when structure*.

Likewise, Dere et al. (2006) argue that rats form an integrated memory of *what, where,* and *when* because rats in their novelty detection experiment showed an interaction between their preference for a recent vs. old and displaced vs. stationary object. If the memory had not been integrated, the rats should have responded to the displacement similarly for both the recent and old objects.

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[8] In human memory studies, Metcalfe, Cottrell, and Menzel (1992) have suggested that explicit memories show bound structure of information, although not specifically *what-where-when* information, while implicit memory shows independent memory representations.

In contrast, Skov-Rackette et al. (2006), discussed earlier, found in their study of pigeon's partial report that the pigeons did not appear to form an integrated memory. The evidence for this was that when two queries were given on the same stimulus presentation, performance on the first test trial (e.g., What was presented?) did not predict performance on the second test trial (e.g., When was it presented?). They argued that this indicates that the pigeons represent each aspect separately. It is possible, however, that like Sperling's (1960) classic partial report study, the pigeons were only maintaining one aspect of memory and forgetting the other aspects once they responded to the initial query for that trial. The other evidence for independence is that there was a dissociation in performance while the animals were learning. The method for the pigeons to report each aspect (*what, where,* or *when*) of a sample was first trained individually in a session and then trained in combination in a session (Skov-Rackette et al., 2006). When the three stimulus aspects were combined in a session, the performance on the *when* aspect declined. Skov-Rackette et al. (2006) argue that such dissociation would not be expected if the stimulus memory was bound into an integrated memory. The Skov-Rackette et al. (2006) argument is concordant with Thorpe and Wilkie (2007) experiment which found that the rats in their study of time-place learning with differential outcomes for correct responses did not seem to store the *what, where*, and *when* information in an integrated memory but rather in a bipartite code, learning an association first between reinforcer quantity and time and later between reinforcer quantity and location.

Although Clayton et al. (2001) emphasized the importance of integration in episodic memory storage, it is not completely clear that this is a necessary characteristic, even in human episodic memory. The research by Wagenaar (1986) suggests that the information about *what, where,* and *when* is recalled by humans differentially and not always all *what, where,* and *when* information is stored*;* this could indicate that elements of episodic memory were not in fact bound into a single memory. Furthermore, it seems difficult to argue that memory of context must be bound to event memories when often much of human spatial and temporal context is the result of later reconstruction from semantic knowledge (e.g., Friedman, 1993; review in Ferbinteanu et al., 2006). Nor does integration of information into unique events seem to magically establish that the information is an episodic memory. One could, for example, remember that Jesse James robbed a bank in Minnesota in 1876 and robbed a train in Missouri in 1879 but these integrated memories are certainly not "episodic" in nature.

Finally, the feature of *flexibility* of episodic memory has been introduced. *Flexibility* allows episodic memory to be used in different situations and updated following new information rather than represented in a fixed way. Clayton, Yu, and Dickinson (2003) argue the scrub jays showed *flexibility* by indicating that they can update their information. Specifically, the birds were given degradation training following a caching episode. In this degradation training, food items degraded at a rate faster than previously experienced; the jays were then able to use this new degradation information to guide their next cache recovery (Clayton et al., 2003).

Babb and Crystal (2005; 2006) also attempted to show *flexibility* of episodic memory in their rats that searched for the replenishing chocolate arm. The rats all experienced devaluation of chocolate by LiCl between initial trials and re-search trials. The rats avoided visiting arms that would contain chocolate after the experience of devaluation. Food was also devalued by testing food specific satiation. Babb and Crystal (2006) trained rats that two preferred food types only replenished after long intervals. The rats were then satiated on one of the two food types after which the rats tended to search the arm that contained the non-satiated food but not the satiated food (Babb & Crystal, 2006). Babb and Crystal (2006) argue that this shows a flexible updating of their episodic memory when new information about the value of food is available. However, as with Clayton et al.'s (2003) study, it is not clear that this *flexibility* feature is a definitional requirement for episodic memory, rather than an emergent property.

In both the scrub jay and rat experiments, the seemingly flexible representation could be semantic or associative in nature. In essence, the scrub jays are showing a time dependent taste aversion. The rat experiments, too, simply incorporate a basic taste aversion induction in which animals are conditioned to avoid foods that caused illness. And, such aversions are well known in non-episodic memory experiments to be able to alter choice responding (e.g., Rescorla, 1992). Furthermore, some evidence that animals can show time-dependent taste aversions has been found (e.g., Moron et al., 2002; Manrique et al., 2004). It is not clear that the poisoning of the chocolate shows flexibility of the episodic-like memory or the generalizability of aversive conditioning to a variety of situations. These tests of *flexibility* would be more impressive if the episodic-like memories themselves were being flexibly applied to a new situation. Tulving (2005) agrees that *flexibility* is not a distinguishing feature of episodic memory, but rather is a feature that is shared by semantic memory. Thus, *flexibility* is a feature of episodic memory, but *flexibility* is not evidence that the memory is episodically represented.

In tests of both scrub jays and rats, both species have shown in some tests that their *what-where-when* memory representations may be bound and flexible. However, the true importance of these features for indicating episodic memory, and their criticality in human episodic memory are still debated.

Some researchers have further argued that the elements of *what*, *where*, and *when* are neither necessary nor sufficient for characterizing episodic memory in animals (e.g., Zentall et al., 2001; Schwartz, Hoffman, and Evans, 2005). Zentall et al. (2001) argued that many episodic memories in humans do not contain information about *where* and *when* an event occurred and that they gather that contextual information through semantic knowledge.[9] Zentall claimed that this makes having the information about all three *what, where,* and *when* elements unnecessary to qualify for episodic memory. Continuing, he pointed out—as we have— that purely semantic memory can contain *what, where,* and *when* without episodic memory of the event (e.g., remembering that the Declaration of Independence was signed in Philadelphia on July 4th, 1776); thus

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[9] This is, of course, supported by Wagenaar's (1986) content research as well.

Zentall claimed that reports of *what, where,* and *when* information, *per se*, are insufficient to qualify the report as evidence for episodic memory (Zentall et al., 2001).

Although Tulving (2002; 2005) has agreed with the insufficiency of *what, where,* and *when* for proving the existence of an episodic memory, we doubt that he would agree that the contextual elements of *what, where,* and *when* events occurred are unnecessary. Tulving indicates that episodic memories have context information including information about what occurred, a general location of occurrence, and at least a sense that the occurrence happened in a past time. And, of course, it has the property of autonoetic consciousness. Without these, the memory is more likely to be an instance of general knowledge or semantically based memory.

Palinscopy

Schwartz, Hoffman, and Evans (2005) argue that some tests of *what, where*, and *when* do not require the animal—or any organism—to think back to the past, but rather could be based on a current representation of the way the world is now (e.g., worms are bad now; chocolate is replenished now). Schwartz et al. (2005) emphasize the importance of using tests that ask the animals to look back in time, termed *palinscopy* by Tulving and Lepage (2000).

Schwartz et al. (2005) tested King, a gorilla, by showing him unique events and then asking him to report at a later time about different aspects of the event, for example pointing at the individual involved or the food that he was given during that event, which is also similar to the test used by Skov-Rackette et al. (2006). Schwartz et al. (2005) view the report about *who* and *what* composed the past event as evidence of episodic memory because there was no present state of the event; instead King had to rely on his knowledge of the past event. Skov-Rackette et al.'s (2006) test of pigeons also requires the birds to "think back" to a previous event and recall which stimulus was presented in a particular location and how long of a delay they experienced to give an answer to the present discrimination. It is not clear, however, whether either Schwartz et al. (2005) or Skov-Rackette et al. (2006) really show *palinscopy* in a way that is distinct from the mechanisms used in any standard delayed matching-to-sample procedures (Hampton & Schwartz, 2004). Delayed matching-to-sample procedures (and non-matching-to-sample) seem to be insufficient as examples of episodic memory and mental time travel because they can be accounted for through mechanisms of familiarity alone. The animal could base its choice on the person or object that is most familiar to them rather than recollecting the past event. However, as more intervening events occur, such as in the case of King, the argument for familiarity declines. While familiarity does not account for the ability to perform symbolic matching-to-sample (SMTS), the animal could either represent the match by associatively activated familiarity or through holding the "match" in mind immediately rather than looking back to the past sample. The same can be said for both Schwartz et al. (2005) and Skov-Rackette et al. (2006). Interestingly, the hippocampus does seem to be involved with at least some tests of delayed matching and non-matching-to-sample, particularly with delays over 15 seconds, in both humans (Monk et al., 2002) and monkeys (Zola et al., 2000).

Experimental alternation studies may be another example of palinscopic episodic memory. In alternation studies, an animal chooses an arm to travel down to receive a reward (or in spontaneous alternation merely for exploration). On the next trial, the animal is required to recall the arm that was last visited and now visit the other available arm, with the next trial switching to the non-visited arm again. Morris (2001) argued that this fails to meet the criteria for episodic memory because the task can be completed on the basis of familiarity of the previously chosen arm. Although this is certainly true of alternation tasks that use short delays, Fortin, Wright, and Eichenbaum (2004) have shown that after a delay of 75 minutes rats do not use familiarity cues to judge whether an odor appeared from an old or new group of odors. It may be that in alternation tasks where only one trial is given per day (Denny & Leckart, 1965; Surridge & Amsel, 1965) that the animals have to use recollection of their last act, which fades at a slower pace than familiarity cues (for human evidence see Yonelinas, 2002). Moreover, it appears that animals tested in delayed alternation tasks show impairment following hippocampal lesions (Winocur, 1991), which is presumed to affect episodic recollection processes but not familiarity (see Fortin et al., 2004).

Unexpected Questions

Besides the possibility of *what-where-when* not necessarily being oriented to the past, some have argued that the integration of *what-where-when* memory may merely represent rule learning (for full critiques, see Roberts, 2002 and Zentall, 2006). It is possible that a series of semantic rules (choose left tray when long delays) could potentially account for the apparent *what-where-when* episodic-like memory and that this type of rule-based learning works more like semantic memory. Strictly, rule based learning alone seems less likely to be occurring in experiments where trial-unique information is used (e.g., Dere et al., 2005a; Ferkin et al., 2008) but does seem to be a problem in experiments where repeated exposures to events occur. Zentall et al. (2001; 2006) proposed that to circumvent the problem of repeated exposures to events, an unexpected question must be used to demonstrate that episodic memory is operative rather than rule based semantic memory. Because unexpected questions cannot be planned for, the animal must "travel back in time" to recall the answer. Zentall gives the example: if someone was unexpectedly asked what they had for dinner, they would have to travel back in time to retrieve the memory of the contents of their dinner from the previous night. If, on the other hand, the person was asked every morning what they had for dinner, the person could use rehearsal mechanisms to create a semantic memory and ensure that they were prepared to answer the question each morning. However, one could imagine that the repeated rehearsal of items could lead to confusion about the specific occurrences. This could mean that episodic memory is necessary or at least beneficial for distinguishing between similar events. For example, a person could remember it was this morning that they had cereal rather than yesterday because they recall running late this morning.

In Zentall et al.'s (2001) view, proper tests for episodic-like memory should consist of an unexpected question that requires the animal to "travel-back" to the experience being asked about.

One way to ask an “unexpected” question in animals is to ask the animal to report on their recent behavior or knowledge. Zentall et al. (2001) showed this ability in pigeons by training them to respond discriminatively to one stimulus by pecking and another stimulus by not pecking. This was the way that Zentall et al. (2001) controlled the animal’s behavior. The pigeons were separately trained to peck one key if they had recently been pecking and another key if they had not pecked recently. The “unexpected question” came about by combining the two aspects of the test so that occasionally during the discrimination trials they were presented with the two keys that “questioned” whether they had been pecking recently. The pigeons accurately responded to this question 68.8% of the time in experiment 1 and 71.9% in experiment 4. Thus, Zentall et al. (2001) found that pigeons could report on whether they had recently been pecking or not even when the pigeon could not anticipate that they would be required to respond about their recent behavior. In a similar set-up, pigeons have also been successfully trained to respond to the unexpected question of *where* they were recently pecking (Singer & Zentall, 2007).

Zentall et al. (2001) were not the first to ask whether pigeons can report on their recent behaviors. Shimp (1982) had pigeons report on the rate of their recent pecking. Pigeons were trained to peck a central key at either a rapid or a slow pace. Occasionally during the session, two side keys would light up at which point the pigeons were required to peck one side key if their previous behavior had been slow pecking or the other side key if their behavior had been rapid pecking. Similarly, Killeen (1978; Killeen & Smith, 1984) found that pigeons can report on whether they caused a key light to go off by their pecking or whether the key light went off on its own (not caused by them). This indicates that the pigeons are aware of their recent behavior as well as the likelihood that behavior caused another event. While the pigeons seem to know what their recent behavior was, it is not clear that these are truly examples of episodic memory, or even of unexpected questions. First, although the birds never experienced the unexpected questions in the discrimination test, they all had plenty of experience answering the question in a very similar context. Additionally, the delays between their behavior and answering the question are short enough that they could be using short-term memory mechanism—or even a feeling of fatigue—rather than the longer-term episodic memories to guide their choices.

Like Zentall et al. (2001), Mercado, Murray, Uyeyama, Pack, and Herman (1998) examined whether animals could report on their recent behavior. Mercado et al. (1998) found that dolphins were able to follow a command to generate a novel behavior— to perform an action that had not been done recently, which in itself requires a memory of recent actions. Mercado et al. (1998) went a step further by training a "repeat" command that required the dolphins to perform an action that they had just completed. Finally, they used the "repeat" command following the command to perform a novel action. This clever task required the animals to reflect on their past behavior rather than just remembering the hand signal that the trainers last gave. The dolphins were quite successful at repeating their recent novel behavior to this unexpected request. Like Zentall et al. (2001), this appears to require episodic memory of recent past events. We must be cautious in interpreting these results, however. If the dolphins had performed another behavior other than the one they had just performed, would they have been wrong? In a sense, there is no wrong answer to the "repeat" command because if they performed a novel behavior it could be argued that they were repeating the "novel" command.

Spontaneous Recall

As in the unexpected questions, spontaneous recall has the advantage of the animals not expecting to be tested on their memory. In a test of chimpanzees, Menzel (1999) hid food in an outdoor enclosure in full view of the chimp. After up to 16 hours, the chimp was given access to a lexigram keyboard on which she had been previously trained. Using the keyboard she recruited a human trainer to help her get outside to the hidden food item; she also correctly indicated the type of food on the keyboard before going outside. Once in the outdoor enclosure, she led the person to the location where the food was hidden. No question was asked of the chimpanzee and no requirement to use the keyboard was made. The chimpanzee, however, had previously been taught to name and to request items. In this case though, the retrieval was unprompted which is more similar to the unsolicited recall of episodic memories in humans.

In combination, the reports on recall of recent behavior and on spontaneous recall may indicate that the animals do have the ability to report on things that happened in their recent past which relates to the palinscopic feature of episodic memory, but whether this is sufficient evidence for episodic memory at this point is not clear.

Autonoetic Consciousness

Because the autonoetic consciousness component is so central to Tulving's view of episodic memory, it is useful to consider some of the pieces that might contribute to autonoesis in animals.

Self Awareness. Like autonoetic consciousness, sense of self is another term that is ambiguous and not clearly defined in human research, let alone animal research. However, both Suddendorf and Corballis (2007) and Tulving (2005) have placed a great deal of emphasis on the importance of a sense of self as a defining aspect of episodic memory. To that end, it is useful to examine what our current knowledge is about animals' sense of self.

One of the earliest tests of the sense of self was the mirror self-recognition (MSR) test (Gallup, 1970). In MSR tests, animals are presented with a mirror and are scored based on their social responses, physical inspection, mirror-testing behavior, and self-directed behaviors. The animals are then marked with paint or dye and observed for any mirror-assisted contact with the mark on their body. To date, a handful of animals have "passed" MSR and/or the mark test including chimpanzees (Gallup, 1970; 1982), gorillas (Posada & Colell, 2007), possibly some cotton top tamarins (Hauser, Kralik, Botto, Garrett, & Oser, 1995), a dolphin (Reiss & Marino, 2001), and an Asian elephant (Plotnik, deWaal, & Reiss, 2006), and now some recent evidence exists for mirror self-recognition in magpies (Prior, Schwarz, Gunturkun, 2008)[10]. The mirror

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[10] There is also the classic study in which Epstein, Lanza, & Skinner (1981) taught pigeons to peck marks on themselves in a mirror. Recently, pigeons have also been found able to learn to peck live video images of themselves and ignore pre-taped images (Toda & Watanabe, 2008).

tests more accurately represent self-recognition in the sense of awareness of one's own body as separate from other bodies, and that one's body is represented in the mirror. These may indicate at least a rudimentary sense of self.

Similarly, Bekoff (2002) has argued that specialized roles in hunting like those seen in some dolphins and wolves represent self-awareness of one's "role" in a group and an understanding of the other group members' roles.

Theory of Mind. "Theory of mind" refers to the concept that an organism recognizes that others have perceptions and/or knowledge that are separate from one's own and that they can hold different (and false) intentions and beliefs. Some have argued there is a connection between sense of self, theory of mind, and episodic memory abilities. Support for such linkage is found in children and adults with Autism Spectrum Disorder, which is known to impair concepts of self and theory of mind, and episodic memory recall while causing no deficits on semantic recall (Crane & Goddard, 2008). Although some have suggested that there is little evidence to suggest a theory of mind in great apes (e.g. Heyes, 1998; Povinelli, Bering, & Giambrone, 2000), there is strong evidence than many great apes and other animal species at least have secondary representations, or the ability to recognize that objects and models can stand for reality (Suddendorf & Whitten, 2001). Although secondary representations may be short of full-fledged theory of mind, they seem to indicate that many of the abilities that appear to be important for theory of mind are present in animals. For example, great apes show the ability to use objects in pretense (e.g., dolls to act out things), recognize events and use information on video displays; more relevant to theory of mind, some great apes appear to understand when actions are intentional and accidental, and they use eye gaze information to determine attention (for review see Suddendorf & Whitten, 2001; see also Povinelli, Theall, Reaux, & Dunphy-Lelii, 2003). Taken together, this collection of skills, particularly the understanding of intentional actions, seems to indicate at least a basic theory of mind. Similarly, dolphins have passed a number of these same tests while elephants and dogs have passed a few (reviewed in Suddendorf & Whitten, 2001).

Dally, Emery, & Clayton (2006) have suggested that scrub jays, too, show a rudimentary theory of mind. When jays cached in front of a conspecific, they were more likely to return later and recache those items that had been observed by the conspecific than the items that could not be observed or when they were not caching in front of a conspecific. Furthermore, the birds recalled which bird had been present at each caching episode and only recached food from the tray that the observer had previously seen; they did not recache food items from the tray that had been monitored by a different observer. Dally et al. suggest that this indicates the jays know that the other bird is capable of stealing the cache and recognize what the observing bird can and cannot see.

Meta-Cognition. The ability of humans to project in time and to have autonoetic consciousness also gives them the ability to think about what they know and remember; this is termed *meta-cognition* (Dere et al., 2006). Rhesus monkeys and apes have also been tested to see if they know what they know. In choice tests, they choose to get more information or refuse memory tests entirely when they do not know the correct answer to a test, but answer immediately when they do know the correct answer (Smith, Shields, Allendoerfer, & Washburn, 1998; Hampton, 2001; Smith, Shields, & Washburn, 2003). Likewise, dolphins will opt out of difficult auditory discriminations, apparently recognizing their own uncertainty about a response (Smith et al., 1995). This is a non-verbal method of expressing meta-memory because it indicates that the animals are aware of their memory contents.

Rats have also been tested on their meta-cognitive ability. Foote and Crystal (2007) tested rats on a tone discrimination task where rats were given the option to either take the test in which a high number of pellets were given if they were correct but no pellets if they were incorrect, or they were allowed to select a lever, called the "uncertainty" lever, that ended the discrimination and gave them an intermediate number of pellets. Foote and Crystal found that rats chose not to take a discrimination test when the discrimination was very difficult. Furthermore, when the option to opt out of taking the test was removed, their performance decreased on the discrimination task suggesting that the rats were in fact judging whether they knew the correct answer and only selecting the option to skip the discrimination test when they did not know the correct answer.

By contrast, a similar test in pigeons showed that the pigeons do not appear to be aware of whether or not they know the correct answer (Sole, Shettleworth, & Bennet, 2003). When the pigeons made pattern discrimination judgments with the option to opt out of the test by selecting an "uncertainty" key, the pigeons, like the rats, tended to select the uncertainty key when the discrimination was difficult. Unlike the rats, overall performance in sessions with the uncertainty key was equivalent to forced choice tests of the discrimination when the uncertainty key was not an option. This indicates that the pigeons were selecting the uncertainty for all hard discriminations and was not a function of their level of certainty on a particular trial. Thus the rats, but not the pigeons, appeared to know when they were likely to make an incorrect answer.

Looking Ahead: Episodic Future Thinking in Animals

Suddendorf and Corballis (1997) have suggested that in addition to allowing us to remember past events in our lives, episodic memory and the assumed mental time travel property endow humans with the ability to project themselves forward into an imagined future (see also Suddendorf & Busby, 2005; Tulving, 2002; Tulving, 2005). Atance and O'Neill (2001) have termed this ability *episodic future thinking*. The two dimensions of mental time travel are also sometimes referred to as *retrospective* and *prospective memory* (for example see Clayton, Emery, & Dickinson, 2006). While retrospective memory refers to the ability to keep track of the past and the record of experienced events, prospective memory refers to the ability to plan for future events and remember what needs to be done (Neisser, 1982; see also Einstein & McDaniel, 2005). There is however a distinct difference between episodic memory and episodic future thinking. Specifically, episodic memory has happened and can be a recording of events while episodic future thinking is necessarily a creation of a possible event based on past knowledge or experiences.

Like episodic memory, episodic future thinking can be contrasted with *semantic future thinking*. While semantic future thinking involves script-like application of knowledge about the future, episodic future thinking involves—in addition— the placement of the self into an imagined context with events and problems that are likely to occur in this possible specific instance, and thus it differs from general semantic predictions of what usually would occur (Atance & O'Neill, 2001). Two requirements for providing evidence of episodic future thinking in animals are: (1) that the behavior be a flexible behavior (removing instinctual examples of preparation such as migration or hibernation), and (2) that the motivational state of the animals' future needs be different than the current motivational state of the animal (removing general operant learning paradigms; Suddendorf & Busby, 2005). Evidence for animal episodic future thinking is mixed. Failures to find it in a given experiment cannot be taken as evidence against episodic future thinking, while individual successes are proof of the availability of the process in that species.

Like episodic memory, episodic future thinking is commonly thought to be a feature of cognition that is unique to humans (Atance & O'Neill, 2001; Suddendorf & Busby, 2005). In many tests of the abilities of animals to plan for the future, animals have shown that they are fairly short-sighted—or at least impulsive. For example, pigeons and rats, but not monkeys, typically choose an immediate smaller reward rather than waiting for a delayed larger reward (for monkeys see Tobin, Logue, Chelonis, Ackerman, & May, 1996; for pigeons see Mazur & Logue, 1978; for rats see Tobin, Chelonis, & Logue, 1993).

In contrast to the impulsive nature of pigeons and rats in delayed reward studies, McKenzie, Cherman, Bird, Naqshbandi, and Roberts (2004) showed that squirrel monkeys could learn to choose the smaller of two available amounts of food following experiences wherein the larger amount of food was pilfered following its selection. Recent evidence in scrub jays and rats also call human uniqueness into question as regards episodic future thinking. Scrub jays appear to show the ability to anticipate the food outcome of their cache searches. When pre-fed with one of two cached foods, jays selectively search in locations where the non-pre-fed food is located (Clayton & Dickinson, 1999b). However, these results are not particularly impressive as anticipation as they do not rule out possible satiation effects that could be accounted for by simpler associative mechanisms (e.g., Holland & Rescorla, 1975). Monkeys and a chimp showed no preference between receiving 5 bananas (an amount that satiates hunger) and 10 bananas, indicating that they had no sense that the extra bananas could be saved for later consumption (Silberberg, Widholm, Bresler, Fujita, & Anderson, 1998) [11]. This example shows a general lack of planning for the future which is considered one of the hallmarks of human episodic future thinking (Suddendorf & Corballis, 1997). The examples where animals were successful may fit into prospective memory; however, they seem to fall short of full-fledged mental time travel because first, relatively short time periods for prospection are involved, and the motivational state of the animal at the time of testing may be guiding their decision rather than a plan for future needs.

In longer term tests of prospective cognition and episodic future planning, Clayton and colleagues found that scrub jays shifted to caching a less preferred food

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[11] Alternatively, this could represent a simpler counting system such as 1, 2, and many. This type of counting is also observed in some human tribal groups. Whether humans with such simple counting systems are indifferent to amounts that exceed that which qualifies as many is uncertain, but unlikely.

item when more preferred food items were either consistently pilfered or degraded at the time of recovery (Clayton, Emery, & Dickinson, 2006). Moreover, the jays seemed to plan for the potential pilferage by re-caching food that had been cached in view of a conspecific. This re-caching behavior occurred only when the jays had previously experienced stealing caches made by other birds (Clayton et al., 2006).

Returning to the "spoon test" proposed by Tulving (2005) or the "rooms task" used in children by Suddendorf and Busby (2005), these tests have been proposed as non-verbal methods of assessing future planning based on "mental time travel". One anecdotal example of an animal passing the "spoon test" involves a chimpanzee named Franje (de Waal, 1982). During one November, the days began to get colder, and one morning, Franje began collecting all of the straw from her cage and began to carry it so that she could make a nest when she went outside. Franje did not seem to do this in reaction to the cold *per se* because she began collecting the straw before she could actually have felt how cold it was outside (de Waal, 1982). No further discussion of this episode was recounted, and because of its anecdotal nature, it must be taken with a grain of salt. Indeed, because she had previously gone outside the days before, and it was starting to get cold, her actions might have been based on a semantic memory of outside temperatures. However, it does suggest the possibility that other animals might be capable of passing the "spoon test."

An experimental test of the "spoon test" was performed by Raby, Alexis, Dickinson, and Clayton (2007). They tested whether scrub jays could plan for tomorrow by preferentially caching food in a compartment in which they did not receive “breakfast” or where they received a different “breakfast” food than the item currently available for caching. The birds were first taught that they would receive a breakfast of powdered foods in one of two rooms. Subsequently, the birds were allowed to cache food items in either of the rooms. The scrub jays preferentially cached food in the room that did not contain breakfast. To control for a tendency to cache in places that are associated with hunger, a second experiment was conducted in which both rooms contained different breakfast foods (e.g., kibble and peanuts). The jays were then given the opportunity to cache one of the two food items (e.g., kibble). Contrary to a conditioning account, which would predict caching food in the same location as the food was previously consumed in, the jays cached kibble food in the compartment where that food was not located at breakfast (e.g., the peanut compartment). If the birds were only concerned with their present need states, they should show no preference for caching in one compartment over another. Instead, they showed an anticipation of where they would want a particular food later. Thus, it seems that the jays could literally plan for breakfast.

Similarly in another analog to the rooms test, Correia, Dickinson, and Clayton (2007) found that the scrub jays could plan to have a “different breakfast”. Jays typically prefer to cache food items that they have not recently been fed. However, the birds shifted to caching the foods that they had just been pre-fed (e.g., pine seeds) if at the time of recovery they were consistently pre-fed the other food type (e.g., kibble). The jays appeared to be altering their present behavior in anticipation of a future desire for another food type. Notably, their future desire was in conflict with their present motivational state.

An experimental application of the “spoon test” was performed by Mulcahy and Call (2006) using bonobos and orangutans. Bonobos and orangutans selected, transported, and saved tools that were necessary to get a reward from an apparatus that they would be able to access at a future time. The bonobos and orangutans had to select a tool from both suitable and unsuitable options in one room and save and transport that tool to a room with the apparatus that contained the food or drink reward. They did this even when there was a 14 hour delay between the opportunity to select the tools and subsequent access to the food apparatus.

Although we are impressed by this future oriented behavior, Suddendorf and Corballis (2008) argue that this does not fully satisfy the requirements of future oriented time travel. Their criticism is that the animals may be acting on a current need state, the desire for the reward, rather than anticipating a future need state. It seems likely however, that much of human behavior that appears to be future oriented actually relies on current desires rather than on desire-free anticipation of future desires. Even in Tulving’s (2005) original description of the spoon test, the little girl could certainly be described as bringing the spoon to bed because of her current desire for pudding.

Consistent with our treatment of episodic future thinking in animals, it is appropriate for us to consider the where the future questions in the study of episodic memory lie. So far the summary of episodic memory as we have discussed it can be reviewed by examining Table 1.

Table 1.

Elements, Features, and Properties of Episodic Memory and Their Discussion in the Human Literature and Examples of Evidence in the Animal Literature[12]

Episodic Memory	**Aspect**	**Human Literature Discussions**	**Animal Literature Examples**
Elements			
	What	Tulving (1972); Wagenaar (1988)	Clayton & Dickinson (1998); Babb & Crystal (2005); Ferkin et al. (2008)
	Where	Tulving (1972); Wagenaar (1988)	Clayton & Dickinson (1998); Babb & Crystal (2005); Ferkin et al. (2008)
	When	Tulving (1972); Wagenaar (1988)	Clayton & Dickinson (1998); Babb & Crystal (2005); Ferkin et al. (2008)
	Who	Wagenaar (1988)	Schwartz et al. (2002, 2005); Dally et al. (2006)
Features			
	Ordering	Healy et al. (2002); Burt et al. (2008)	Fortin et al. (2002); Schwartz et al. (2005)
	Binding	Metcalfe et al. (1992)	Clayton et al. (2001); Dere et al. (2006)
	Flexibility	Tulving (2005)	Clayton et al. (2003); Babb & Crystal (2005, 2006)
Properties			
	Autonoetic:	Tulving (2002, 2005)	
	Self	Tuvling (2005); Suddendorf & Corballis (2007)	Gallup, (1970, 1982); Posada & Colell, (2007)
	Theory of Mind	Suddendorf & Corballis (2007)	Review in Suddendorf and Whitten (2001); Dally et al. (2006)
	Meta Cognition	Suddendorf & Corballis (2007)	Foote & Crystal (2007); Smith et al. (1998; 2003); Hampton, (2001)
	Future Planning	Tulving (1985a, 2005)	Raby et al. (2007); Correia et al. (2007); Mulcahy & Hall (2007)
	Palinscopy	Tulving & Lepage (2000)	Zentall et al. (2001, 2006); Schwartz et al. (2005)

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[12] This table is intended to be illustrative not exhaustive of the examples in the human and animal literature.

Filling in the Holes: Future Experiments and Questions to Answer

From the human and animal literature on episodic memory, it is clear that there is no real consensus on the single “true” definition of episodic memory or even the importance of any given element, feature, or property of episodic memory. The many aspects of episodic memory all contribute to the experience of episodic memory, but it is far from clear which aspects constitute the true core to the concept of episodic memory. Is it possible to have an experience of mental time travel and autonoetic consciousness without also accessing information about *what, where,* and *when*? Conversely, can a person have the rich and detailed content information of a specific past event without feeling as though they are re-experiencing it? By parsing out the different aspects of episodic memory, we can gain an understanding of which are essential to episodic memory as well as the relationship of the features to each other.

Much of our human literature relies on artificial tests of list learning with fewer studies examining the more naturalistic experiences of episodic memory. Furthermore, most tests of human subjects rely on language to convey the presence of episodic memory. If episodic memory does not require language to be expressed, then certainly non-verbal tests of adult episodic memory should be possible—and need to be developed and used experimentally. In particular, development of an objective measure of autonoetic consciousness in humans would help us to assess its presence in other species as well as pre-verbal children. We suggest that it could be particularly informative to try and recreate for humans some of the animal tests of episodic memory. More detailed tests of human patients with episodic memory deficits on episodic-like memory tests would help to clarify how humans might solve a given task with or without episodic memory capabilities. For example, Tulving (2005) proposes that a dog recovering a buried bone in the backyard does not require the use of an episodic memory because the dog does not remember the event of burying a bone. The question is, though, could the patients K.C. or N.N. retrieve something they hid when they lack the ability to orally report or recall even that they had visited the location previously? Could they learn to avoid looking for "degraded" foods like the scrub jays? If these human patients, with supposedly intact semantic memories, are incapable of using their semantic knowledge to solve episodic-like memory tasks, it would be difficult to claim that non-human animals are solving the problem with semantic memory. That is we believe that the challenge has now shifted from the researchers who use animals and become one for the researchers who use humans.

If, as Conway (2002) has suggested, episodic memory's function is for tracking goal attainment, we should be able to test this in both humans and animals by examining the ability to track interrupted goal attainment in individuals with intact and disrupted episodic memory. For example, one could test whether an amnesiac individual can recall that they have finished eating lunch or completed a crossword puzzle and compare it to the recall of task completion by normal individuals. By understanding the function of episodic memory, we can better design experiments to test for its presence in other species.

So where do we currently stand in our knowledge about animals and episodic memory? Table 1 gives a breakdown of the elements, features, and properties of episodic memory that various people have suggested are important and also the species that have shown evidence for each. It is important to note that for nearly every noted element, feature, or property hypothesized to be a constituent of episodic memory, an existence has been found in at least some animals. The exception is *autonoetic consciousness* which is defined in such a way that absent high level verbal skills it cannot be detected. The evidence reviewed for each constituent of *autonoetic consciousness* is not always as clear, particularly for self-awareness and theory of mind, but there is at least some evidence that animals have rudimentary capabilities in each. Thus, the search for evidence of episodic memory in animals is not a fatuous exercise, and claims that it is are meretricious. There are also no clear neurobiological reasons for supposing that humans are unique in their episodic memory.

When we begin to put the pieces of this puzzle of episodic memory in animals together, it seems a new picture is emerging. At least for some species—especially those with a large hippocampus, the evidence that they have capacity for episodic memory is falling into place.

Non-traditional laboratory species, particularly social and very bright species, such as dolphins and elephants seem like a great place to seek to expand episodic memory research.

Because substantial segments of the literature on human deficits and animal episodic-like memory (particularly, the primate research) are based on case studies of a small number of individuals, replication of prior observational reports and small experiments (e.g., with King) would help to improve our confidence and our understanding of whether these episodic abilities and deficits are unique to the individuals tested or are really more general capabilities.

The addition of more naturalistic studies could help to clarify the extent that episodic memory exists in the everyday lives of animals. For example, we might look at other species of caching birds such as tits and chickadees (Krebs, Healy, & Shettleworth, 1990) or look at food caching mammals such as squirrel species (Devenport, Humphries, & Devenport, 1998), deer mice (Meyers-Manor unpublished data), or kangaroo rats (Jacobs, 1992) to see whether elements of episodic memory can be found in them as well. Beyond caching, we might expect to find episodic-like memory in species that have to keep track of changes that occur in other animals across weeks or months. For example, the ability of the polygynous meadow voles to track the reproductive state of its mates across different parts of its territory (Ferkin et al., 2008), suggests we could examine the ability of cowbirds or cuckoos to track the reproductive state of several different host birds (Sherry, Forbes, Khurgel, & Ivy, 1993). In the search for an appropriate model for testing treatments for the loss of episodic memory, it would also certainly be beneficial to develop a model and methodology that could be tested quickly and on a larger scale than many of the tests of episodic-like memory in animals. Developing operant tasks that mimic episodic-like memory tasks could help to meet this need.

Furthermore, a number of questions require further evidence to bolster isolated findings. In particular, more examples across a range of species tested on the “spoon test” or the “rooms task” would help to clarify the ability of animals to plan for future needs meeting a criterion for mental time travel. The extension of Lubinski and Thompson (1987) or Cowey and Stoerig (1997) for the development of tasks that could allow animals to report on subjective experiences of remembering would also be ideal, but certainly challenge experimenter ingenuity. Animal experiments that involve combining tests of different elements of episodic memory, such as unexpected questions about context detail, would help to build confidence in purported animal models of episodic memory.

Seeing the Big Picture: Conclusions

Both human and animal studies show that there is no single uniformly accepted method of testing for episodic memory. Each methodology elucidates different aspects of our concept of episodic memory. The evidence from animals indicates that at least some animals have the ability to flexibly use an integrated memory of *what-where-when* to solve problems. Furthermore, animals can report on their recent past experiences as well as respond in planful ways for their future needs. Although there is no test to be certain that animals experience these events as humans do, through autonoetic consciousness, this does not necessarily preclude animals from having episodic memory or at the very least episodic-like memory. The evidence is mounting that much of the memory contents of at least some species of animals parallels the structure of human episodic memory and uses parallel brain structures. Although the progress in understanding episodic memory in animals has come a long way, there is still much work left to be done—especially as to form, content, and generality of episodic memory.

Perhaps, as more evidence comes in about episodic memory in humans and animals, Tulving will extend his definition once more to include animals' recall of events in his picture of episodic memory. Then, as we lay out the last pieces of our puzzle, we will discover once more that humans are not as unique as we thought we were.

Chapter 2: Remembering When: Pigeons Can Recall What-Where-When based on Time of Day

In the previous chapter, the potential for and evidence of episodic-like memory in a variety of animal species was established. Several tests of episodic memory were discussed. For the present thesis, the methodology used follows in the path of many animal researchers by examining animals' memory of *what-where-when.* As we move into the remaining chapters of the thesis, I hope to demonstrate the ability of pigeons to show *what-where-when* memory based on two different time perceptions, when during the day and how long ago, and to test the *flexibility* of their *what-where-when* memory. The first two experiments are included in this chapter. The first experiment tests *what-where-when* based on *when* events occur during the day: morning or afternoon. The second experiment tests the *flexibility* of this *what-where-when* information in a novel test. The next three experiments are included in the following chapter and examine *what-where-when* based on how long ago previous events occurred and the *flexibility* of this knowledge.

In an ever changing world, the ability to track *where* and *when* significant events occur is beneficial to a variety of animal species. The purpose of the present study was to assess the presence of this ability to track *what-where-when* memory in pigeons based on *when* during the day the events occurred. In this study, pigeons were trained to discriminate between two foods that required a differential number of pecks to obtain and produced differing food access (*what*), making one more “attractive” than the other. The birds were required to alter their choice of keylights (*where*) to get these differential foods based on the time of day (*when*). Pigeons were able to choose the key that required fewer pecks in the morning and then switch to the opposite key in the afternoon sessions to maintain the choice for the “attractive” food with fewer pecks indicating a *what-where-when* memory. However, the pigeons failed to transfer this knowledge to a novel situation, showing limited *flexibility* in use of the learned *what-where-when* information.

Remembering When: Pigeons Can Recall What-Where-When based on Time of Day

Episodic memory, the ability to recall personal life events, is a central part of human existence. When people experience deficits in episodic memory, such as those caused by Alzheimer's disease, it can be devastating to social interactions, personal motivation, and general functioning in the world (see review in Reichman & Negron, 2001). The impetus to find an animal model for episodic memory and understand the extent to which animals share our cognitive capacities has led to a great deal of research into examining the elements of episodic memory in non-human animals.

The term episodic memory was first coined by Endel Tulving (1972) who described it as memory that "receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events" (p. 385). He contrasted this form of memory with semantic memory, a memory for facts that have no specific context associated with them. Tulving (1983) later expanded on his initial definition that focused on context to include the concept of *autonoetic consciousness,* which is one's awareness of one's own existence in subjective time. With this new addition, Tulving (1983) also proposed that episodic memory was unique to humans because animals have not shown any evidence of *autonoetic consciousness*.

In response to Tulving's (1983) challenge that only humans can have episodic memory, Clayton and Dickinson (1998) coined the term "episodic-like" memory to refer to animals' memory of events in a particular context but with the recognition that it is currently impossible to show autonoetic consciousness in non-verbal species. Thus, episodic-like memory research in animals shifted the emphasis back to the remembrance of particular events in time and space.

Because all biologically significant events occur in both space and time, one would predict that the tracking of both spatial and temporal dimensions of such events would be beneficial to the animal. In fact, both Gallistel (1990) and Wilkie (1995) proposed that at each occurrence of a biologically significant event, whether appetitive or aversive, three pieces of information are recorded automatically by the animal: the nature of the event, the location of the event, and the time that the event occurred. This hypothesis led to the study of time-place (*when-where*) learning in animals, which examined the ability of animals to recall *when* and *where* events occurred. The extensive literature on time-place learning in animals partially confirms the prediction that animals can track the time and location of important events. Time-place learning has been found to some extent in a variety of species including insects, fish, birds, and rats (for reviews of relevant studies see Wilkie, 1995 and Carr & Wilkie, 1999).

Many initial studies into time-place learning involved bird species. Naturalistic observations of oystercatchers, a shore-bird, found that they were capable of anticipating mollusk availability based on the time of day, which was correlated with tidal rhythms (see review in Wilkie, 1995). The oystercatchers would not appear near the mussel bed until low-tide. Similarly, laboratory studies of birds have found time place learning in pigeons (Saksida & Wilkie, 1994), warblers (Biebach, Gordijn, & Krebs, 1989; Biebach, Falk, & Krebs, 1991), weavers (Falk, Biebach, & Krebs, 1992) and starlings (Wenger, Biebach, & Krebs, 1991). Saksida and Wilkie (1994) found that pigeons could discriminate which of four keys would produce food at a given time. Two keys produced food for each pigeon; one key was active in the morning while the other was active in the afternoon. The remaining two keys never produced food. During the first minute of each session, none of the keys produced food. The number of pecks to each key during this non-reinforced time period was recorded. The pigeons learned to peck at the appropriate keylight based on whether the session was a morning or an afternoon session. Furthermore, Saksida and Wilkie (1994) showed that these animals were not merely relying on alternation but were showing use of circadian rhythms by having the birds skip either a morning or afternoon session. The pigeons maintained accurate pecking to the appropriate keylight even following a skipped session. These laboratory studies have indicated that birds can use circadian rhythms to predict the location of food availability. It is likely that both time related cues, such as position of the sun or timing of light cycles, and intrinsic timing methods can be and are used by the birds (see discussion in Saksida & Wilkie, 1994).

Studies of time-place learning in rats have been more mixed than those on birds. While several studies failed to find time-place learning (Thorpe, Bates, & Wilkie, 2003; McDonald, Hong, Ray, & Ralph, 2002), others have had more success (Carr & Wilkie, 1999; Carr, Tan, & Wilkie, 1999; Pizzo & Crystal, 2004), particularly when there is a response cost associated with a wrong choice (Widman, Gordon, & Timberlake, 2000).

Although not explicitly varied in most time-place studies, the animals must also have at least some recognition of *what* occurs in the time and space, typically the availability or lack of availability of food. The contextual components of episodic-like memory described by Clayton and Dickinson (1998) involve recalling *what* happens, *where* something happens, and *when* something happens. While this is quite similar to Wilkie's (1995) description of animal's memory for events, research on episodic-like memory has focused more on varying *what* occurs. Rather than remembering that food is available at a time and place, episodic-like memory tests have attempted to show that animals can recall which specific quality of foods are available, and when they are available to be obtained. Indeed, Thorpe and Wilkie (2007) were able to show that rats could use differential amounts of food to perform *what-where-when* discriminations following repeated daily trials.

As with the initial research on time-place learning, research on episodic-like memory also began by studying birds. Clayton and Dickinson (1998) tested a group of scrub jays on episodic-like memory. Scrub jays are a caching, food hiding, species that store and recover both perishable and non-perishable foods. Taking advantage of this natural predisposition, Clayton and Dickinson (1998) had the jays cache two food types, wax worms and peanuts. The jays preferred to eat the wax worms, but over time, the wax worms would "rot". Thus if it had been only a short time (4 hours) since the birds had cached the wax worms, they should search preferentially in the locations where they had hidden the wax worms. In contrast, if it had been a long time (124 hours) since the birds had cached the wax worms, they should search preferentially for the peanuts given that the wax worms were now rotten. This was, in fact, the pattern that the scrub jays showed, indicating a recall of *what* food was hidden, *where* it was hidden, and *when* the food was hidden.

Since Clayton and Dickinson's (1998) seminal paper on scrub jay episodic-like memory, many people have attempted to reveal the components of episodic-like memory in a variety of species. Subsequent papers on the scrub jays have confirmed that the jays can show *what-where-when* learning (e.g., Clayton & Dickinson, 1999a; 1999b; Clayton, Yu, & Dickinson, 2001; deKort, Dickinson, & Clayton, 2005). Similarly, magpies have shown the ability to track *where* and *when* they cached different food items (Zinkivskay et al., 2009). Furthermore, Clayton and colleagues have been able to show that the jays store the content information in a single integrated event memory and can use that information flexibly in new situations (Clayton et al., 2001; deKort et al., 2005). They argue that these additional criteria further the connection between episodic-like memory in animals and human episodic memory.

As with time-place learning, experimenters working with rats have shown some successes (e.g., Babb & Crystal, 2005; 2006; Naqshbandi et al., 2007) as well as some failures (e.g., Bird et al., 2003; McKenzie, Bird, & Roberts, 2005) in uncovering the *what-where-when* content of episodic-like memory. Similarly, studies on monkeys have so far failed to find recall of *what-where-when* (Hampton, Hampstead, & Murray, 2005); however chimps and gorillas have shown recall of all three elements individually and various combinations of two elements (e.g., see Menzel, 1999; Schwartz & Evans, 2001; Schwartz et al., 2002; Schwartz et al., 2005).

In a return to avian species, Skov-Rackette, Miller, and Shettleworth (2006) studied episodic-like *what-where-when* learning in pigeons. In their study, Skov-Rackette et al. (2006) presented pigeons with a stimulus of a particular shape, presented in one of eight locations, and with a retention interval of 2 seconds or 6 seconds. The pigeons had to answer questions following the presentation of the stimulus by pecking at the matching shape, location, or symbolically matching the time component with one symbol representing the 2 second retention interval and another representing the 6 second retention interval. However, the pigeons struggled with the *when* component and seemed to be representing each element of the event separately rather than in a bound event memory.

Our present study attempts to combine the traditions of time-place learning and episodic-like memory by examining the ability of pigeons to recall *where* they have to peck in order to get a specific kind of food (*what*) depending on *when* it is during the day. Because pigeons have been remarkably successful at tracking *where* and *when* food is available (Saksida & Wilkie, 1994) as well as their ability to recall *what-where-when* information of a sample stimulus (Skov-Rackette et al., 2006), it seems quite likely that pigeons would also be successful at tracking *what* food outcome is associated with the *where* and *when* (Experiment 1). Pigeons are a useful species to study because they have been used extensively in learning and memory experiments (e.g., see Carter & Werner, 1978). Likewise, the use of operant chambers to test the animals allows this experimental method to be adapted to a variety of laboratory situations and species. In our experiment, unlike Skov-Rackette et al.'s (2006) study, the pigeons will be unable to hold independent representations of the event context, but must combine all three elements in order to correctly choose the food location at a given time of day. If only one component was represented at a time, they could not know *where* to peck to get the most food (*what*) based on *when* that keylight-food outcome was made available. Furthermore, we hoped to test in a follow-up experiment, as Clayton et al. (2001) and deKort et al. (2005) did, whether pigeons could show flexibility in their use of the episodic-like memory by applying their *what-where-when* knowledge to a novel situation (Experiment 2).

Experiment 1

Initially, birds were trained to peck at colored keylights that were located on either the right or left side of the chamber (*where*). In the terminal training and thereafter, pecking of each keylight received a different type of food reward and each food reward required different amounts of effort in order to get that food. The differences in reinforcer quality, quantity, and required effort constituted the *what* component of the reinforcers. Finally, the relationship between the keylight color/position and the food/effort contingencies were switched between morning and afternoon sessions (*when*). Thus, pecks to the left, blue keylight may have gotten them plain seed with little effort in the morning, but in the afternoon pecks to the left, blue keylight produced cherry seed and required substantial effort.

With these contingencies in place, a pigeon would demonstrate knowledge of *what, where,* and *when* by choosing the appropriate keylight (*where*) that predicted the preferred and easier to get food (*what*) based on whether it was morning or afternoon (*when*). Assessment of this *what-where-when* knowledge was performed in a non-reinforced choice test between the two colored keylights at the beginning of test sessions occurring both in the morning and the afternoon. We hypothesized that pigeons would switch the keylight that they pecked for based on the time of day in order to minimize the effort required and to maximize the food reward.

Method

Subjects

The experiment used 13 homing pigeons, retired breeders from Vern Thorson (Henning, MN). They were individually housed in wire cages with a 12:12 light and dark cycle. The pigeons were maintained at approximately 85% of their free-feeding weight. All pigeons that dropped below 85% of their free feeding weight received supplemental feeding in their home cages 30 minutes after the last session of the day. Pigeons were given *ad libitum* access to water and grit.

One pigeon was removed from the study because it was never able to establish reliable keylight pecking for food reward. Additionally, two birds had to be removed during the course of the study for health reasons. This left ten birds that completed the entire study.

Apparatus

The pigeons were trained and tested in standard commercial Med-PC operant chambers with Plexiglas side-walls and aluminum ceiling, front-, and back-walls. The dimensions of the chamber were 46 cm x 46 cm x 58 cm (L x W x H). On the front wall of the chamber, 17.5 cm above the floor and 12 cm away from each other were two response keys (diameter 2.5 cm) that were illuminated from the back. Also on the front wall were two rectangular openings (5 cm x 5.5 cm), through which the food hoppers, located outside of the chamber, could deliver the subjects' food. The openings were vertically aligned in the center of the front wall, between the two keylights. The bottom hopper was 3 cm above the floor, whereas the top hopper was 21cm above the floor. The house light was located in the upper left corner of the back wall. Two small speakers that emitted either a tone or a buzzer were centered on top of each other along the back wall of the apparatus. Each chamber itself was located within a sound-attenuating box (Med- Associates, VT), which contained a speaker that emitted a masking white noise at 80 dB during all sessions, so that subjects could not hear any sounds coming from outside of their box. These boxes were, in turn, in a sound insulated room separate from the programming equipment. The chamber was operated by Med Associates interfacing and Med-PC software (Med Associates Inc., VT) and a personal computer.

Procedure

All birds were given 3 days of habituation to the testing apparatus in which they were placed into the chamber for approximately 20 minutes first in darkness and then with the house light on. Subsequently, all sessions started with an adaptation period that included 2 minutes of dark followed by 2 minutes of light. After this, the house light turned off for 10 seconds, and then turned back on, signaling the start of the first trial in the session, which occurred 8 seconds after the house light turned back on. Between each trial the same lighting procedure was used: the lights turned off for 10 seconds, and then turned on, signaling the start of a trial in 8 seconds. Yellow and blue colored keylights were used for all sessions.

Autoshaping of Operant Response. Pigeons were first trained to peck the keylights through an autoshaping procedure. Initially, sessions were given only in the morning. In this training, the blue keylight always appeared alone on the left side of the chamber or the yellow keylight always appeared alone on the right side of the chamber. This was done to establish the color and location together as the *where* component. During these morning sessions, the presentations of the blue keylight were followed by cherry flavored seed, and the presentations of the yellow keylight were followed by normal bird seed for half of the birds; the reverse relationship was used for the remaining birds (determined by random selection). In the autoshaping, the keylight was presented for 8 seconds followed by the presentation of the appropriate food. However, if pigeons pecked the keylight twice at any time during the 8 second keylight presentation, food would be delivered immediately. Each food was presented via the food hopper for 5 seconds during this phase. Autoshaping sessions initially included 50 trials. On all 50 trials either a blue or yellow light was presented randomly, typically resulting in 25 blue trials and 25 yellow trials per session.

Location Learning. Once the pigeons began consistently pecking the presented keylight and eating the food presented, which took on average 9 sessions, the pigeons were shifted to a location choice task. These sessions were only offered in the morning as well. The pigeons were presented either two yellow keylights or two blue keylights on each side of the chamber. Only one side (the correct side) would be reinforced by the corresponding food—pecks to the other side would not be reinforced, but instead would lead to a correction procedure. The correction procedure consisted of withholding reinforcement, turning off the house light, and repeating the trial. For the blue keylight the correct side was the left key, and the yellow keylight had the right key as the correct side. These sessions contained 52 trials each—26 with the presentation of yellow keylights, and 26 with the presentation of blue keylights, which were randomly scheduled throughout the session.

Choice Trials. After subjects chose the correct keylight color and location combination on at least 80% of trials for two consecutive sessions, which took on average 16 sessions of location training, choice trials were added. These sessions still occurred only during the morning. Four of the 52 trials, presented randomly through the course of the session, were devoted to presenting the pigeons with both a blue keylight (on the left) and a yellow keylight (on the right) simultaneously. They were reinforced appropriately for pecking either keylight. This was done not only to prepare the pigeons for later choices between the two stimuli that would occur during test sessions, but also to establish which response-food combinations the subjects preferred.

Time of Day Learning. When the birds maintained 80% correct on location with choice trials for at least two days, which took on average 37 sessions, they were moved to two sessions per day to introduce the time discrimination. Sessions were offered in both the morning and the afternoon. Morning sessions were run between 8 A.M. and 10 A.M, while afternoon sessions were run from 2 P.M. to 4 P.M. Birds were run in the same order in their morning and afternoon sessions so that the 6 hour time between sessions was equivalent from day to day. The order of running birds, however, was random across days. In the afternoon, the opposite of the location-food contingency offered in the morning was in effect. Thus, if an animal had to peck the yellow keylight on the right in the morning to get normal seed, they would now have to peck the blue keylight on the left to get the normal seed. As with the morning session, this was counterbalanced, so that all birds experienced the reversal of the keylight-food contingency from morning to afternoon sessions. Other than this difference in the keylight color-location to food contingency, afternoon sessions proceeded just as morning sessions. However, the number of trials was reduced in both the morning and afternoon, so that there were 24 of these location trials and 4 choice trials per morning and afternoon session. In this phase of training, a partial reinforcement schedule was introduced in both AM and PM sessions. This was done to maintain persistence and counter extinction effects that might be engendered by non-reinforced test trials. Each session, morning and afternoon, had 4 non-reinforced trials among the 28 session trials, or approximately 1 in every 7 trials.

Because all but one of the pigeons showed no significant preference between foods, but rather a preference for the location of the keylight that they pecked, we introduced additional differences in the food consequence to make this aspect of the experiment more salient to the subjects. Specifically, one food was made available for 6 seconds, while the other was only available for 3 seconds. Additionally, the "short-duration" food also required more keylight pecks, fixed ratio 13 (FR 13), than did the food that was exposed for longer, which required only 3 pecks (FR 3). This created a response preference in subjects. The FR schedule and the length of food delivery corresponded with a particular food (plain or cherry seed), counterbalanced across subjects. Therefore, which color keylight (yellow or blue) required more pecks and produced shorter food availability reversed from morning to afternoon sessions. Birds experienced on average 31 days of this time-of-day training before experiencing a memory content test.

Memory Content Test. Testing in this stage consisted of two unreinforced choice trials presented at the beginning of the session. Like the choice trials during the session, these choice trials consisted of the presentation of a blue keylight on the left side of the chamber and a yellow keylight on the right side of the chamber. The test trials were presented at the beginning of the session so that the subjects could not use other trials to judge which keylight would require fewer pecks and lead to a preferred food consequence. Therefore, the subjects would have to rely on previous learning about time of day as it relates to the keylight-response contingency in order to peck in the correct location at that time of day and make the response that should yield their preferred food outcome. During these test trials, subjects were required to peck the keylight only two times, and they were not rewarded for responses to either keylight. After the two test trials, the session followed as typical, with 24 location trials and 4 choice trials. Sessions with memory-content tests were done in pairs, with either (a) a test session first done during the morning and second in the afternoon of the same day, or (b) with a test session first done in the afternoon, and another done second in the morning of the following day. On the type (b) pair, no morning session preceded the first afternoon test. This pairing arrangement was done as a check on whether or not session order and the time allowed between test sessions had an effect on test performance. There were at least two training sessions between each test pair.

Data Analysis

Data about keylight pecking were coded such that for all birds the “optimal-morning” key referred to the key that was “Easy/Long delivery” in the morning, and it was then “Hard/Short delivery” in the afternoon. Thus, the counterbalancing of key color (blue or yellow) to “Easy/Long delivery” was combined for analysis purposes. All analyses compared the number of pecks to this coded “optimal-morning” key at either morning or afternoon sessions. Using the coding to the “optimal-morning” key allowed us to track the change in their pecking behaviors across the morning and afternoon sessions. Repeated measures ANOVAs were conducted using SPSS to compare key pecking behavior toward the “optimal-morning” key at the two time of day points and the order of morning and afternoon memory-content sessions.

Results and Discussion

If pigeons were showing knowledge of *what-where-when* memory, they should show a decrease in pecking to the optimal morning key between the morning and the afternoon sessions. The pigeons did in fact show a change in their key pecking behavior based on the time of day. In the morning, the birds pecked the “optimal morning” key 55% (SE= 13.3) of the time. However, in the afternoon, they pecked this same (now non-optimal) key only 32.5% (SE=9.16) of the time. This change in behavior across the time of day was significant (F(1, 9)=5.651, p=.04). There was no significant difference in the order of the tests (i.e., whether morning test sessions were followed by afternoon test sessions or whether morning sessions were skipped and afternoon test sessions were followed by morning test sessions; F((1, 9)=.043, *ns*) and no interaction between time of day and order of test sessions (F(1,9)=.101, *ns*). Figure 3 shows the key pecks to the key that is optimal in the morning session based on time of day and the order of the presentation of tests.

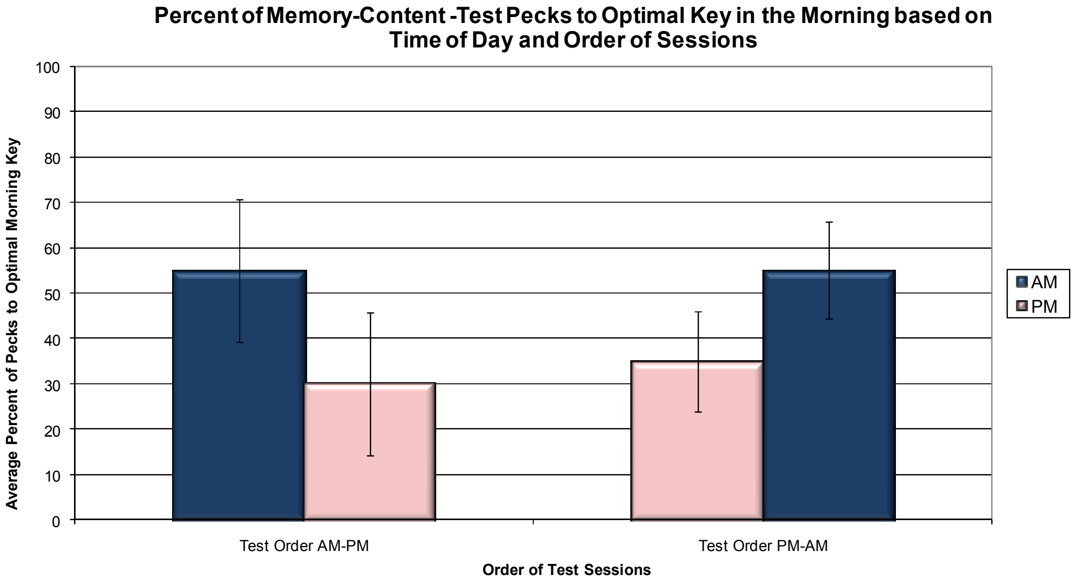

Figure 3. This illustrates the percent of pecks to the optimal morning key based on the time of day and the order of the test sessions. Error bars represent standard error.

Based on these results, it is clear that the birds changed *where* they pecked based on the time of day, morning or afternoon (*when*), in order to maximize their food outcomes with minimum effort (*what*).

Experiment 2

The goal of Experiment 2 was to continue to establish memory for ‘what’, ‘when’, and ‘where’ in our subjects, but also to go beyond this by also assessing the potential flexible use of these information components by the pigeons. To explore the pigeons’ ability to use information about *what, where,* and *when* flexibly, we included a transfer-of-control procedure, by which predictive information learned from separate Pavlovian conditioning is introduced into the operant setting (e.g. Overmier & Leaf, 1965; Bull & Overmier, 1968). This procedure is appropriate for this experiment because it can demonstrate the use of learned behavior and knowledge applied to novel information; such transfer procedures have been used successfully with pigeons and with experiments involving multiple conditioned stimuli and multiple reinforcer outcomes (e.g., Overmier, Ehrman, & Vaughn, 1983).

Following the training of the ‘what’, ‘when’, and ‘where’ contingencies in Experiment 1, these same pigeons were introduced to Pavlovian conditioning trials, which paired the previously used foods (‘what’) with different sounds. Utilizing a transfer-of-control procedure, the sounds were then used to prime responses from the pigeons by presenting the Pavlovian cues thus creating an expectation for a specific food consequence (*what*). In Experiment 2, a pigeon could demonstrate the flexibility criterion of episodic-like memory by anticipating the food outcome predicted by the sound cue and then pecking the correct keylight location (*where*) that corresponds with that food based on the time of day (*when*). We hypothesized that pigeons would in fact be able to vary their pecking behavior according to the anticipation of a reinforcer (e.g., after hearing a buzz that predicts cherry seed, peck blue in the morning but yellow in the afternoon; after a tone that predicts normal seed, peck yellow in the morning but blue in the afternoon). Pigeons would take the information from the sound cue, which refers to a specific food, and then peck the key that corresponds to this food, which changes based on time of day. Thus, key pecking would depend not only on the auditory food cue, but also on time of day, because both had a relation to the correct key pecking.

Method

The subjects and apparatus used in Experiment 1 were also used in Experiment 2. Furthermore, the start of Experiment 2 coincided with the introduction of the Time-Food Contingency Manipulation in Experiment 1, meaning that both the operant and the Pavlovian phases were simultaneously taught to the subjects. The procedural steps in this experiment built on the procedural steps of the previous experiment. During progression through the following procedural steps, subjects continued to undergo sessions described under the Time of Day Learning and Meaning-Content Test subsets, while gaining the information necessary for the Transfer-of-Control Test in Experiment 2.

For this experiment, the sound cue was either a tone or a buzz, which signaled delivery of either the normal bird seed or the cherry flavored bird seed in a Pavlovian relation.

Procedure

Pavlovian Conditioning. Pavlovian conditioning sessions were introduced some weeks after the afternoon time-of-day sessions had been implemented. These Pavlovian sessions immediately preceded every “Time of Day Learning” session—that is to say, Pavlovian conditioning sessions occurred once in the morning and once in the afternoon, immediately before the start of each operant session. A tone or a buzz was presented for 4 seconds which was followed by a .5 second delay and the presentation of normal seed or cherry seed with the food’s corresponding delivery length, either 3 or 6 seconds. The relationship between the sound cue and food outcome was fixed across sessions and unlike the keylight food contingency did not change from morning to afternoon sessions. These contingencies were counterbalanced in subjects—such that some birds received cherry flavored seed after the tone, and in other trials received normal seed after buzz trials, and vice versa. These two conditioned stimuli were each always presented in separate trials, and never simultaneously in one trial. Each sound was presented three times per session, for a total of six sound conditioned stimuli trials per session. Between each Pavlovian trial the same inter-trial interval as in Experiment 1 was in effect, with 10 seconds of dark followed by 8 seconds of light before the next stimulus presentation. The sounds were presented in a random order throughout the session. On average, birds spent 97 days experiencing the morning and afternoon sessions with Pavlovian conditioning trials before they were tested on the transfer-of-control.

Transfer-of-Control Test Sessions. The test trials included the presentation of either the tone or buzz for five seconds. After five seconds the yellow and blue keylights were presented as in a typical choice trial. These keys remained lit until one received two pecks. After this, the house lights were turned off, and a new trial period began. Four such test trials were randomly interspersed with the six typical Pavlovian conditioning trials. Of the four test trials, two trials started with the presentation of the tone, and the other two trials started with the presentation of the buzz. Test sessions were offered both in the morning and afternoon. Note that the Pavlovian trials only signaled to the bird which food was predicted by the sound cue and did not give any indication of the relationship of the keylights to the foods. The transfer-of-control test trials were non-reinforced so that there would be no indication of a “correct” or “incorrect” response in the transfer-of-control test. Following the test trials and Pavlovian trials, the normal operant sessions previously described in Experiment 1 were administered. Sessions including transfer-of-control test trials were always done in pairs, with some of the pairs beginning with a morning test session and another test session in the afternoon of the same day, and others beginning with an afternoon test session, and another test session administered in the morning of the next day. Much like in Experiment 1, testing was done in pairs in order to ascertain the effect of test session order compared to time of day alone on pecking performance. There were at least two days in which testing did not occur between each test pair.

Data Analysis

Data about key pecking were coded for comparison of behavior across birds. Thus, for all birds the coding was done so that one auditory cue predicted the “easy/long” food item and could be achieved by pecking the “optimal morning” key, as was done in Experiment 1. All choices were converted into percent of pecks to the “optimal morning” key. Repeated measures ANOVA’s (2x2x2) using SPSS were employed to compare the percent of pecks to the “optimal morning” key based on the presentation of tone or buzz, the time of day, and the order of the test session.

Results and Discussion

If the birds were showing flexible application of their *what-where-when* memory to the Pavlovian sound cues, they should peck the key that predicts the same food outcome as the sound cue in the morning and the opposite key in the afternoon, producing an interaction effect between sound cue and time of day on key pecking behavior. More specifically, we would expect that for pigeons that heard the tone cue which, for example, predicted plain seed (with long presentation and little effort), they would peck the key associated with that food at that time of day. The birds would hear the tone and peck the left/blue key in the morning and the right/yellow key in the afternoon. The opposite would be true with the buzz which predicted cherry seed (with short presentation and high effort) and would require a right/yellow peck in the morning and a left/blue peck in the afternoon. By contrast, if the birds were not being flexibly cued by the tone and buzz, we would expect that they would revert to pecking based solely on the time of day as in Experiment 1.

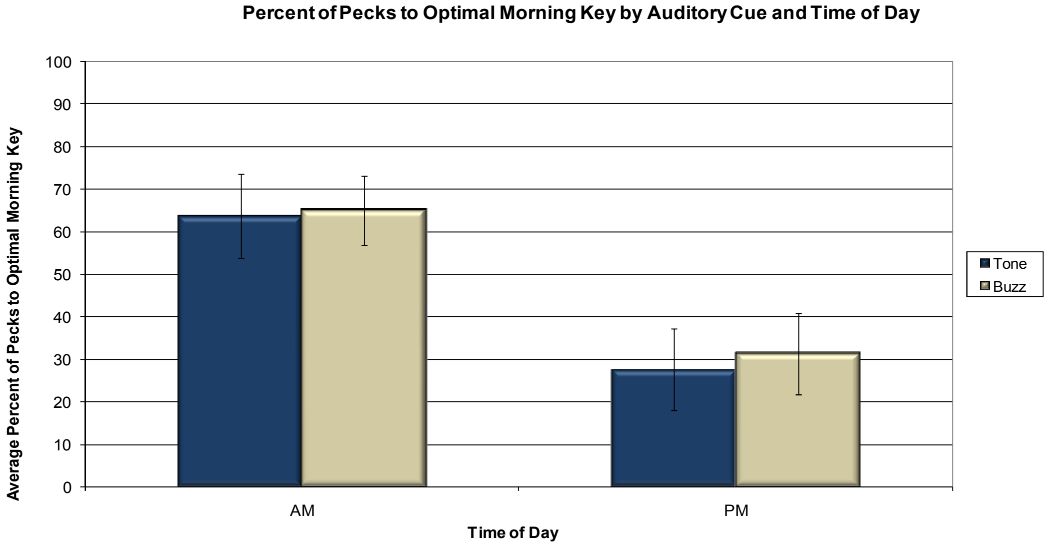

Figure 4. This figure illustrates the percent of pecks to the optimal morning key based on the tone and buzz presentation and the time of day. Error bars represent standard error.

The results of Experiment 2 indicated that the pigeons showed little change in behavior based on the presentation of the tone and buzz with no difference in the number of pecks to the left/blue key when the tone or buzz was presented (F(1, 9)=.878, *ns*) and no interaction between the presentation of the tone and buzz and the time of day (F(1,9)=.063, *ns*). Figure 4 shows the response of the birds to the tone and buzz based on the time of day. As is clear from figure 4, there was a significant change in key pecking in response to the time of day with significantly more pecks to the left/blue key in the morning (M=64.38, SE=8.49) than in the afternoon (M=29.38, SE=9.37; F(1,9)=15.31, p=.004). Thus, although the birds ignored the tone and buzz cues, they continued, as they did in Experiment 1, to respond to the “easy/long” presentation of food by changing their pecking behavior from morning to afternoon as appropriate to the operant contingencies without regard to the presentation of the Pavlovian information.

General Discussion

Both Experiment 1 and Experiment 2 confirmed our hypothesis that pigeons are able to alter their choice preferences in order to choose the location (*where*) that has the most food and lowest response cost (*what*) based on the time of day (*when*). Both experiments showed a change in behavior from morning to afternoon sessions (Fig. 3). Similar to the outcomes of Saksida and Wilkie (1994), the results from Experiment 1 indicate that the birds are able to track the time of day based on circadian rhythms. When sessions were skipped, the birds were still able to choose the key that predicted the “easy/long” food delivery indicating that they were not using a mere alternation strategy. Unforutnately, they did not show differential responding as a result of the Pavlovian cues that had been associated with the different foods and durations of food access (Fig. 4).

Some may argue that this test of pigeons represents a test of *what-where-when* memory but fails to meet the criteria for episodic or even episodic-like memory. We tend to agree that this task has the potential to be solved by semantic and rule-based mechanisms. However, given the arguments strongly made by Tulving (e.g., 1985a; 2002; 2005) that episodic memory is a hierarchical system that relies on a functioning semantic memory system, we believe that it is useful to establish abilities—even semantic ones---for *what-where-when* learning before attempting to find more trial unique episodes. Surely, if animals fail to track the *what-where-when* of repeated events, it is highly unlikely that they will be able to do so for trial unique episodes.

We believe that work in this area should continue in a variety of directions. First we think that research on other forms of timing should be done. For example, can the pigeons show the "how long ago" timing that has been shown in scrub jays (Clayton & Dickinson, 1998; 1999) and rats (Babb & Crystal, 2005, 2006)? Next, we believe that attempts should be made to show longer-term memories for unique events, thus transferring this *what-where-when* task into a more episodic-like task.

In terms of other elements of episodic-like memory, Experiment 2 failed to show *flexibility* of *what-where-when* knowledge in the transfer-of-control task. The fact that the pigeons failed to show a transfer-of-control of influence from our Pavlovian trials on the operant behaviors is disappointing. It is perhaps not surprising given that the pigeons showed no real distinction between the food qualities of cherry versus plain seed. There was no differential effort directly associated with the Pavlovian trials. Under the circumstances, the transfer-of-control would have required an anticipation of the quality and quantity elements of outcomes to over-ride the element of effort by selecting sometimes against the "easier" key associated with the time of day. In this situation, the birds chose to continue to select the key that was associated with minimal effort (as well as greater quantity and specific quality) rather than the one associated with the food predicted by the Pavlovian stimulus. Future attempts to show transfer-of-control in a similar situation would do well to select more distinct and unique outcomes with a greater difference in preference. Alternatively, flexibility could be shown through applications of previous knowledge about events to novel situations by transferring the timing of events, such as deKort et al.'s (2005) food rotting rates, to novel keylight contingencies.

It is likely that there will be no single experiment that will illuminate the episodic memory abilities in animals. Rather, we will take many baby steps in the hopes of sneaking up on this complicated phenomenon. We feel this research has made another step forward in understanding how capable pigeons are at tracking events and context, which in turn can help us understand memory systems in general to a deeper extent. As the evidence for episodic-like memory in animals grows, we hope that useful models of human episodic memory can be created to better aid in treatment and prevention of episodic memory loss.

Chapter 3: Not So Bird-Brained: Pigeons Can Recall What-Where-When Based on How Long Ago

A variety of animal species have been tested on episodic-like memory for foraging events. Many of the most successful tests have been done in food-caching bird species. The present series of experiments looked at the ability of pigeons, a non-caching species, to track differential food degradation as a function of elapsed time using an operant choice task. The first experiment tested the ability of pigeons to track *when* a food, earned by a spatial choice, "rotted" based on how long ago they were last trained. The second experiment added a food "ripening" condition for the birds to track. Finally, the third experiment examined whether the pigeons' "knowledge" of "rotting" and "ripening" could be applied flexibly to new response choices. Importantly, pigeons showed the ability to change their foraging patterns based on information about food "rotting" and "ripening", but did not show any evidence that they could use this information in a flexible manner. These findings suggest that pigeons have abilities to track *what-where-when* events as do caching birds and other animal species, but perhaps represented in a more rigid manner.

Not So Bird-Brained: Pigeons Can Recall What-Where-When based on How Long Ago

As we move through our daily lives, we take moments to reminisce about what happened in our day or to recall a long past experience. These moments of remembering are commonplace and very central to our experiences as human beings. The loss of these cherished memories due to disease or injury can be devastating both for the individual and their family and friends (e.g., see review in Reichman & Negron, 2001). In the past decade, the search for these life experience memories, termed episodic memory (or "mental time travel") in animals has surged. Understanding the extent and nature of episodic memories in animals could allow us to create models of human memory loss and to gain a better understanding of the evolutionary function of such a memory system.

The term episodic memory was first defined by Endel Tulving (1972) as memory for distinct events in a spatial and temporal context. This contrasts with semantic memory which is a memory system for facts and general knowledge and tends to produce context-free memories (Tulving, 1972). Tulving (1983) expounded on his initial definition to include the personal experience that often accompanies episodic memories. He termed this personal experiential component, *autonoetic consciousness*. Specifically, autonoetic consciousness refers to the way that episodic memories are experienced as events that happen to oneself. Because of the conscious experience that occurs in episodic memory, Tulving (1983) also proposed that episodic memory is a memory system that is unique to humans.

Without clear definitions and ways to test consciousness in animals, let alone autonoetic consciousness, Tulving (1983) seems to have defined animals out of the picture. However, animal researchers were not content to leave the issue at that. Many researchers turned their attention to finding evidence of memories for events in time and space—a return to Tulving's original definition (1972). Recognizing that this definition failed to meet the full experiential criteria for human episodic memory, animal researchers have termed this memory of distinct events in time and space as "episodic-like" memory (Clayton & Dickinson, 1998).

The study of the ability of animals to track events in time and space has come from two different areas of research. The first has examined animals learning about time-place contingencies. In "time-place learning" studies, animals are asked to track biologically significant events (typically food acquisition) that change locations based on the time of day. Time-place learning has been observed in the wild (e.g., see Wilkie, 1995) as well as in laboratory settings (e.g., Saksida & Wilkie, 1994; Carr & Wilkie, 1999) in a variety of species such as insects, fish, birds, and rodents (for review see Carr & Wilkie, 1998).

Many of the first studies into time-place learning focused on birds. In the wild, oystercatchers, a shorebird, have been observed to track the availability of mollusks based on the time of day (review in Wilkie, 1995). Likewise, hummingbirds can use time of day cues to help them track when flowers in particular areas have replenished their nectar and are now ready to be eaten from (Henderson, Hurly, Bateson, & Healy, 2006). Similarly, laboratory studies of birds have found strong evidence of time place learning in pigeons (Saksida & Wilkie, 1994), warblers (Biebach et al., 1989, 1991), weavers (Falk et al., 1992) and starlings (Wenger et al., 1991). It is likely that both time related cues, such as position of the sun, and intrinsic timing methods, such as circadian rhythms, can be and are used by the birds. However, a recent study has indicated that pigeons more readily use endogenous circadian rhythms than external cues such as changing artificial light source (Petruso, Fuchs, & Bingman, 2007).

Unlike the birds studied, rats seem to struggle with time-place learning. Several studies of rats have failed to find time-place learning (e.g., Thorpe, Bates, & Wilkie, 2003; McDonald, Hong, Ray, & Ralph, 2002), but others have had more success (e.g., Carr & Wilkie, 1999; Carr, Tan, & Wilkie, 1999; Aragona, Curtis, Davidson, Wang, & Stephan, 2002; Pizzo & Crystal, 2004), particularly when there is a response cost associated with a wrong choice (Widman, Gordon, & Timberlake, 2000).

Like time-place learning, research on episodic-like memory has attempted to look at animals' ability to track events in time and space. There are two main differences in the research on time-place learning and episodic-like memory. The first difference is that episodic-like memory studies have used multiple food outcomes to try and more explicitly test animals knowledge of *what* happens at a given time and place. The second difference is that episodic-like memory studies have most commonly used "how long ago" events occurred to test animals' memory rather than a time point within a day (morning versus afternoon). Pigeons have previously been found to be able to use information about *what* events occur *where* based on when during the day the event occurs (see Experiment 1 and 2)

As with time-place learning, the birds seem to more readily demonstrate their episodic-like knowledge of temporal and spatial relationships than rodents do. Research on episodic-like memory in rodents has yielded mixed results with some failures (Bird et al., 2003; McKenzie, Bird, & Roberts, 2005) and several recent successes (Babb & Crystal, 2005, 2006; Naqshbandi et al., 2007; Ferkin et al., 2008). Researchers have also struggled to find a bound *what-where-when* event memory in primates (e.g., Hampton, Hampstead, & Murray, 2005); however, all of the elements have been demonstrated individually as well as various combinations of *two* elements (e.g., see Menzel, 1999; Schwartz & Evans, 2001; Schwartz et al., 2002; Schwartz et al., 2005).

In a key study involving scrub jays' episodic-like memory, Clayton and Dickinson (1998) looked at the jays' ability to remember how long ago they cached different food items. Specifically, Clayton and Dickinson (1998) had jays hide either wax worms, the jays' preferred food, or peanuts in different caching trays. The jays then were returned to the cache locations either a short time (4 hours) or a long time (124 hours) after their initial caching of the food. Following a short time delay, both food items remained fresh and the jays recovered the wax worms at a higher rate than the peanuts. After the long delay though, the wax worms had now become "rotten" and were no longer edible so the jays preferentially recovered the peanuts rather than the wax worms. Thus, the jays seemed to recall *what* food item had been hidden, *where* that food item was hidden, and *when* that food item had been hidden. Subsequent papers on the scrub jays have further supported these initial findings of *what-where-*

when learning (e.g., Clayton & Dickinson, 1999; Clayton, Yu, & Dickinson, 2001). The scrub jays have also shown that their episodic-like memories are bound into a single event memory and can be flexibly used in a new situation and updated following new information (Clayton et al., 2001; deKort et al., 2005). To test flexibility in the jays, deKort et al. (2005) gave jays new training about the rates that food items degraded. The jays were able to take the new information about quicker food degradation rates and apply it to their temporally based cache recovery. Like the scrub jays, magpies, another member of the corvid family, have been found to recall *when* and *where* they previously cached different food items (Zinkivskay, Nazir, & Smulders, 2009). The magpies learned to retrieve one color of food pellets from an open caching maze only after a short delay and the other color of food pellet only after a long delay.

Pigeons, a non-caching bird species, have also been tested for their episodic-like memory. Pigeons were asked to recall *what-where-when* elements of a stimulus that was presented to them on a video board (Skov-Rackette, Miller, & Shettleworth, 2006). The pigeons had to recall the shape of the stimulus, the location that the stimulus was presented, and the retention interval (2 or 6 seconds) between the stimulus presentation and the answer options. The pigeons struggled to recall the *when* component and seemed to represent each of the stimulus elements separately rather than in a bound event memory.

In a slightly different approach to episodic-like memory, Zentall and colleagues (2001, 2007) have examined pigeons' ability to recall their recent past behavior. Pigeons were asked to indicate whether they had recently been pecking (Zentall et al.,

2001) or the location at which they had recently been pecking (Singer & Zentall, 2007). Pigeons were able to report on their memories of their recent behavior. The emphasis for these experiments was to test recall for what recently occurred rather than to test recall of the context of a specific event.

Given the success of using pigeons in time-place learning and some success in episodic-like memory studies, it is likely that pigeons could show episodic-like memory in a bound event using methods similar to those of Clayton and Dickinson (1998). In the present experiment, we hoped to call on the traditions of both time-place learning and episodic-like memory to create a task to demonstrate pigeons' memory of *what-where-when.* Pigeons could prove to be a useful model for episodic-like memory tests because of the long history of using them in learning and memory studies (e.g., see Carter & Werner, 1978) that provides a large knowledge base of their behavior. They also provide an interesting test of an avian species that does not cache food. Emery and Clayton (2004) have suggested that scrub jays may provide a somewhat unique example of episodic-like memory because of the evolutionary pressures for food caching and recovery of perishable food items. While pigeons, and many other species, do not have the need to recall where hidden food is located, there are still many evolutionary pressures that would seem to encourage the development of episodic-like memory systems. For example, many food sources have limited temporal availability across the day or across seasons. The ability to recall when foods are available or when they have ripened (or rotted) should improve the fitness of that animal.

In the present experiment, we tested pigeons' ability to track the "rotting" of food items (Experiment 3) and then the "ripening" of food items (Experiment 4) as a function of how long ago they had previously experienced that food. Previously in our lab, pigeons were shown to track *what* food outcomes were available from a particular location (*where*) based on *when* during the day (morning or afternoon) the pigeons were encountering the locations (see Experiments 1 and 2). For the present experiments, we used another approach to the *when* element of episodic-like memory. Like in Clayton and Dickinson (1998), the *when* element involved recalling how long ago a food event was experienced. This approach to *when* provides a more discrete event memory than recalling *when* in the day different events occur. Finally, we also hoped to demonstrate that the pigeons could use their acquired *what-where-when* knowledge flexibly in a new choice situation (Experiment 5), an ability that they failed to show in a previous experiment (see Experiment 2).

Experiment 3

Pigeons were trained to peck colored key lights in an operant chamber. These key lights represented *where* the food items were located. Each key light color (red or green) was thought of as a distinct foraging patch that the pigeon had to use to gain access to the food outcome. The key light was paired with one of two distinct food outcomes: black sunflower seeds or cracked corn. These distinct food items represented the *what* element. Finally, the element of *when* was added by making the birds' preferred food item rot over time. Thus, as with Clayton and Dickinson (1998), when the delay between events was short, both foods remained fresh, but following long delays, the preferred food tasted bad. A pigeon that preferred black sunflower seeds could show their *what-where-when* knowledge of events by pecking the key that leads to black sunflower seeds when a short delay between sessions occurred but pecking the key for the corn when the long delay had caused the black sunflower seeds to become rotten.

Method

Subjects

The experiment used 9 homing pigeons, retired breeders from Vern Thorson (Henning, MN). They were individually housed in wire cages with a 12:12 light and dark cycle. The pigeons' were maintained at approximately 85% of their free-feeding weight. All pigeons that dropped below 85% of their free feeding weight received supplemental feeding in their home cages 30 minutes after the last session of the day. Pigeons were given *ad libitum* access to water and grit.

All birds had experience with keylight pecking and hopper training.

Apparatus

The pigeons were trained and tested in standard commercial Med-PC operant chambers with Plexiglas side-walls and aluminum ceiling, front-, and back-walls. The dimensions of the chamber were 46 cm x 46 cm x 58 cm (L x W x H). On the front wall of the chamber, 17.5 cm above the floor and 12 cm away from each other were two response keys (diameter 2.5 cm) that were illuminated from the back. Also on the front wall were two rectangular openings (5 cm x 5.5 cm), through which the food hoppers, located outside of the chamber, could deliver the subjects' foods. The openings were vertically aligned in the center of the front wall, between the two keylights. The bottom hopper was 3 cm above the floor, whereas the top hopper was 21cm above the floor. The house light was located in the upper left corner of the back wall. Each chamber itself was located within a sound-attenuating box (Med- Associates, VT), which contained a speaker that emitted a masking white noise at 80 dB during all sessions, so that subjects could not hear the actions of other subjects in neighboring boxes. These boxes and their chambers were, in turn, in a sound insulated room separate from the programming equipment. The chamber was operated by Med Associates interfacing and Med-PC software (Med Associates Inc., VT) and a personal computer.

Procedure

The procedure was implemented in several stages described below. In each stage, the session began with a habituation period which included 2 minutes of dark followed by 2 minutes of light before the session began. Following habituation and between each trial, the inter-trial interval began with the houselight being extinguished for 10 seconds and then lit for 8 seconds signaling the start of a trial. The two hoppers in the chamber contained two different types of food: black sunflower seeds and cracked corn. These two foods were selected for the differences in color, texture, and flavor. Pilot studies indicated preferences between these two very distinct types of food were equally distributed across the nine birds, with five birds preferring the black sunflower seeds and four birds preferring the cracked corn. One of the birds refused to eat any of the black sunflower seeds even under the deprivation schedule. This bird was changed to a nut blend that included sunflower seeds. All references to black sunflower seeds for this bird will refer to the nut blend.

Initial Training. As aforementioned, all of the birds had previous experience with pecking at keys and receiving food in the operant chambers. For this experiment, novel keylight colors were used. Thus, to initiate pecking to this novel keylight color, the birds were placed on an autoshaping procedure in which one of the two keylights was lit, either red or green, for 8 seconds. If the birds did not initiate pecking during the keylight illumination, the food was delivered after the completion of the 8 seconds. If the birds pecked the illuminated keylight, the food was delivered immediately after their second peck to a light. The delivery of food was 5 seconds in duration and was always signaled by the presentation of a hopper light. The relationship between the color of the keylight and the food outcome was counterbalanced across the birds such that for some birds pecking the red keylight always delivered black sunflower seeds while pecking the green keylight always delivered cracked corn, and vice versa for the other birds. The relationship between the keylight color and food outcome was constant throughout the experiment for a given bird. During the autoshaping program, 26 trials were given each session. For 24 of the trials, only one keylight color was presented at a time and the side of the presentation was counterbalanced so that each keylight appeared on each side an equal number of times. This was done to prevent side preferences from guiding their behavior. The other 2 trials involved a choice between red and green keylights with side counterbalanced. Pecking the keylights during the choice trials resulted in the appropriate reinforcement for that keylight color. If no pecking occurred during the choice trials, no food reinforcement was given and the session moved to the next trial. Choice trials were used to prepare the birds for later choice tests and to continue to assess their food preferences.

Once the pigeons were reliably pecking at both the red and green keylights and eating both foods from the two hoppers, which took approximately 6 sessions, the birds were moved to a graduated set of programs. The three stages of the training involved the presentation of 24 randomized trials per session with the criteria that each keylight color would be presented on each side of the chamber for 6 trials. For each pigeon, these sessions lasted approximately 20 minutes. During training, all sessions were performed once daily between 11:00AM-12:00PM or 2:00PM- 3:00PM; whether they were run starting at 11:00AM or 2:00PM was randomly determined across days. The pigeons were run in groups of three in a random order during the one hour time period.

The first stage of training involved the use of a variable ratio schedule (VR3) in which on average 3 pecks earned food reinforcement, with a range from 1-5 pecks. Pigeons were moved to the next program when they pecked with average latencies between keylight presentation and completion of 1-5 pecks of less than 5 seconds. This took 5 sessions on average. Following the VR3 program, the pigeons were moved to a VR5 program with an average of five pecks (range of 1-9 pecks) required for each food reinforcement. When the pigeons' latencies were less than 5 seconds on the VR5, which took on average 4 sessions, they were moved to the final training program a

VR7, which required on average 7 pecks with a range of 3-11 pecks. They experienced 11 days of one session per day on the VR7 schedule before beginning time training.

Time Training. During the VR7 stage of training, an additional type of trial was added as well as a second daily session. First, four non-reinforced trials, one for each color in each side position, were added to maintain persistence in pecking and to counter extinction effects that might be engendered by later non-reinforced test trials. These additional non-reinforced trials replaced four of the normal trials described above leading to a total of 26 trials per session.

The birds continued to receive their initial session of the day from either 11:00AM-12:00PM *or* 2:00-3:00PM, but they also received an added a session from 3:00-4:00pm each day. The birds were run in the same order within a given day. Thus, the pigeons always either experienced a 1 hour delay or a 4 hour delay between their first and second session of the day. The pattern of delay across days was chosen randomly. The second session of the day was similar in set-up to the first session of the day with both red and green lights presented randomly across the 24 trials including 4 non-reinforced trials presented, but during the second session no choice trials were presented.

Baseline Tests. After 11 days of time training with both foods remaining good, baseline testing of behavior was done to determine what the birds' initial responses were after each of the two delays between sessions. At this point, the pigeons had no experience with either type of food going bad. These baseline test sessions always took place during the second session of the day and that session was at a set time of day. On test days, the birds were run in their first daily session as normal. The first session occurred either 1 hour or 4 hours prior to the test session. Test sessions began with 10 choice test trials. The test choice trials consisted of the presentation of both the red and green lights simultaneously. The side on which each light was presented was counterbalanced and randomly presented across the 10 trials. Once the pigeons pecked three times to a given keylight, a choice was recorded and the program moved to the next test trial following a variable inter-trial interval ranging from 18 to 28 seconds. No reinforcement was given for pecks to either keylight during these tests. If no pecks occurred to either keylight within 10 seconds, which was over two standard deviations above the mean latency, then the trial was restarted following the variable inter-trial interval. If a bird did not peck either keylight for at least 4 trial presentations in a row, the program was progressed to the next trial and that trial was recorded as a non-choice trial. Following the 10 test trials, an abbreviated version of the normal second daily session began, with only a single keylight presented per trial and no choice or non-reinforced trials presented for a total of 16 trials. The baseline test sessions were performed two times at each of the 1 and 4 hour time delays in a counterbalanced order. There were a minimum of two normal training days between each test session.

Food Rotting. After the tests of baseline behavior, pigeons were trained such that their preferred food "rotted" over time. The change was in the keylight-food contingency obtained in the second session of the day and was based on how long ago the first session occurred. If the first session had been recent (1 hour delay), then both food items remained fresh and edible. If, on the other hand, the first session had been long ago (4 hours), then the pigeon's preferred food item had now become "rotten" while the previously non-preferred food item remained fresh. The food was made "rotten" by mixing in 1 teaspoon of Sunlight lemon scented dish soap per ounce of food. In pilot studies, the addition of soap was found to nearly eliminate food consumption even in food deprived pigeons. Because the soap did produce a distinct smell, at this stage of training, we began to place a dime sized dot of soap on the paper towels that lined the bottom of the operant chamber. The soap was placed just below the food hoppers in all sessions that the birds experienced so that they could not use the smell of soap as an indication of the choices to make in a given session.

In the second session of the day, the birds were still required to peck the green and red keylights on a VR7 schedule to receive the food outcomes. However, if the bird did not peck the keylight within 8.5 seconds, which was two standard deviations above their average latencies in this phase, the bird received no food delivery and was moved onto the next trial following the standard 18 second inter-trial interval. The pigeons were tested after they were consistently showing an avoidance of the "bad" food item and maintained latencies of less than 5 seconds between stimulus onset and completion of pecking during the first sessions; the pigeons experienced on average 19 days of pecking for rotten food in training before experiencing test sessions.

Rotten Food Test Sessions. As in the baseline test sessions, tests sessions for the learning about "rotten" food always took place during the second session of the day. On test days, the birds were run in their first daily session as normal. The first session occurred either 1 hour or 4 hours prior to the test session. Test sessions were shortened to 8 test trials to counter possible extinction effects from the non-reinforced test trials. Test sessions on the “rotten” food were repeated three times for each time delay, run in a counterbalanced order with at least two training days between each test day. In all other respects, the “rotten” food test sessions were the same as the baseline test sessions.

Data Analysis

For each test session in both the baseline and “rotten” food tests, the percent of pecks to each keylight, red or green, was recorded. The data were then converted such that all percentage of pecks was in terms of pecks to the preferred food item that eventually became “rotten” following the long delay. Separate repeated measures ANOVA’s were performed on the data for the baseline and for the “rotten” food tests using the type of preferred food (the one that rots after long delays) as a between subjects factor with the time delay between sessions and each replication of the test sessions as within subjects factors. For all analyses, the criteria for significance was $p<.05$.

Results and Discussion

If pigeons were showing knowledge of *what-where-when* contingencies of the “rotting” food in this experiment, we would expect to find a significant effect of the time delay between sessions, but no real effect of the preferred food type or the replication of test sessions.

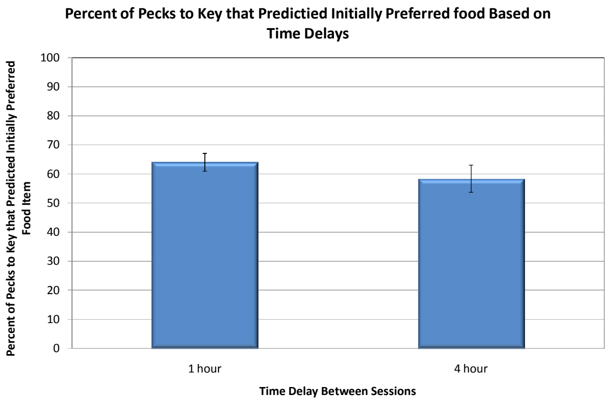

Figure 5. The figure illustrates the baseline tests of percentage of pecking to the keylight that predicted the initially preferred food outcome based on the time delay between sessions. Error bars represent standard error.

Initially, the birds were tested before the birds had any experience with food going bad through the addition of soap. The birds showed no significant difference in the number of pecks to their preferred food item (i.e., the item that would begin to rot later) at short delays between sessions (M=64.00, SE=3.05) and at long delays (M=58.38, SE= 4.66; F(1, 7)= 2.03, *ns*). Figure 5 illustrates the overall lack of change in keypecking during these baseline tests. Additionally, the birds showed no change in the keys they pecked across the two sessions that they were tested, the food that they preferred, or any interactions of these factors (All F's<4.2, *ns*; see Appendix A for breakdown of F values).

Once the food was made to "rot" at the 4 hour time delay, the birds showed a change from their baseline behavior. The birds showed both a general suppression of their responding to their preferred food as well as a temporally specific larger decrease in behavior due to the "rotting" of their preferred food. Specifically, they decreased their overall responding to their preferred food, showing a general suppressive effect of experiencing soap with percent of pecking to their previously preferred food decreasing from a mean of 64 (SE=3.05) in baseline tests at 1 hour to 35 (SE=5.20) at 1 hour once they experienced the food rotting. Similarly, the pecking to the previously preferred food declined from 58.38 (SE=4.66) to 20 (SE=5.67) following the tests at 4 hours. More importantly for this experiment there was a temporally specific suppression of responding. The temporally specific effect indicated that the birds pecked for their previously preferred food more when the food was good following the short delay (M=35, SE=5.20) than when the food was bad following the long delay (M=20, SE=5.67) and this within phase change in pecking behavior between 1 and 4 hour delays was significant (F(1, 7)=19.77, p=.003; see Figure 6). There were no significant differences in pecking based on which food went bad for a particular bird, either black sunflower seeds or corn, although the decrease for rotten black sunflower seeds was numerically larger (F(1, 7)=3.74, p=.09). All other comparisons including the replication of the test sessions and interactions between session replications, which food went bad, and the time between sessions showed no significant difference in pecking behavior (all F’s<1.85, *ns*).

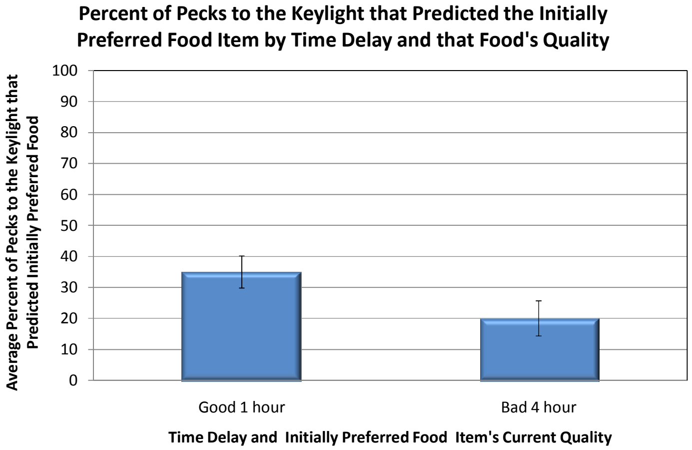

Figure 6. The figure illustrates the percentage of pecking to the keylight that predicted the initially preferred food item based on time delay. During the 4 hour delay, the preferred food item has become “rotten” and is no longer tasty. Error bars represent standard error.

The birds decreased their pecking to the key that predicted the “rotten” food at the long delay. Additionally, the birds showed a general decline in preference for the “rotten” food. This is not surprising because of their moderate initial preference for the food item (around 60%) and their repeated experience of this food “rotting” while the other food item remained good at all time points. Importantly, the pigeons showed a change in behavior from their baseline pecking behavior and in the distribution across keys that accessed the different foods following delays. Specifically, at the baseline measurements, the birds showed no difference in choice behavior across the two time points. In contrast, following the initiation of the food “rotting” procedure, the birds discriminated between the two time points. This result shows that the pigeons integrated *what, where,* and *when* under the “rotten” conditions to guide their choice behaviors as a function of time since the last exposure to that food.

Experiment 4

Experiment 4 expanded on Experiment 3 by including a “ripening” of foods. In the wild, animals are likely to experience foods that rot when left too long, but they are also likely to experience foods that must be returned to at a later point before they are edible (“ripening”). For this experiment, the same food item that was designated as the one that decayed or “rotted” in Experiment 3 continued to be used. Additionally, the other food item was made to be “bad” at short delays but then “ripened” into a good food following long delays. Thus, at each time delay, one food was “bad” while the other food was “good”. The purpose of this experiment was to show that the pigeons could track multiple time, location, and food quality relationships. If the pigeons were showing *what-where-when* memory in this experiment, they would show a change in the key light (*where*) they were pecking based on *when* they last experienced a session, which determined the quality of the food outcome earned.

Method

In Experiment 4, all of the subjects and apparatus are the same as in Experiment 3. The basic procedure is also the same as in Experiment 3 except as described below.

Procedure

For this experiment, we added another temporally based food quality change to track. The food that was previously good at all time points was now degraded for the second session following short delays from the first session (1 hour) but not long delays (4 hours); this quality degradation was completed by the addition of soap, using the same method as in Experiment 3. At each time delay, one of the food items remained fresh and one food item was "bad". Thus, for a given bird, one food item degraded only following the 4 hour delay and the other food item was bad only following the 1 hour delay. All other methods for both sessions are the same as those described in Experiment 3. The birds experienced 25 days with each food going bad at each time delay before testing. As in Experiment 3, all choice test sessions were unreinforced and each of the time delays, 1 hour and 4 hour, were tested three times each in a counterbalanced order, with at least two intervening non-test days.

Data Analysis

For this experiment, the data were coded in terms of the percent of pecks to the key that predicts the initially preferred food (i.e., the food that goes bad after a 4 hour delay). Repeated measures ANOVA were used to compare the time between sessions and the repetition of test sessions as within subjects factors and the preferred food of the birds as a between subjects factor.

Results and Discussion

As in Experiment 3, we would expect to see a change in the percent of key pecks to the color that predicts the preferred food item based on the time delay between sessions. We would expect this effect to be more dramatic than in Experiment 3 because of the "ripening" effect of the non-preferred food item. In Experiment 4, the birds showed much stronger changes in behavior in this experiment than in Experiment 3. The pigeons pecked at the key that predicted "good" food following the 1 hour delay much more often (M=77.08, SE=5.83) than when that key predicted "bad" food following the 4 hour delay (M=33.13, SE=6.47) and they pecked at the key that predicted "good' food at 4 hours delay more (M=66.87, SE 6.47) than when that key predicted bad food at 1 hour (M=22.92, SE=5.83). This change in pecking behavior was significant (F(1, 7)=29.32, p=.001). Figure 7 presents the changes in behavior based on the time delay and which food was bad at that time delay. The pigeons also showed an improvement in their adaptive choices in the discrimination test over the three test sessions with each successive test session showing more differentiated responding; this difference between sessions was significant (F(2, 14)=4.80, p=.026). All other comparisons including the comparison of the groups based on their preferred food and all interactions with food preference, repetition of sessions, and the time between sessions were not significant (All F's <1.83, *ns*).

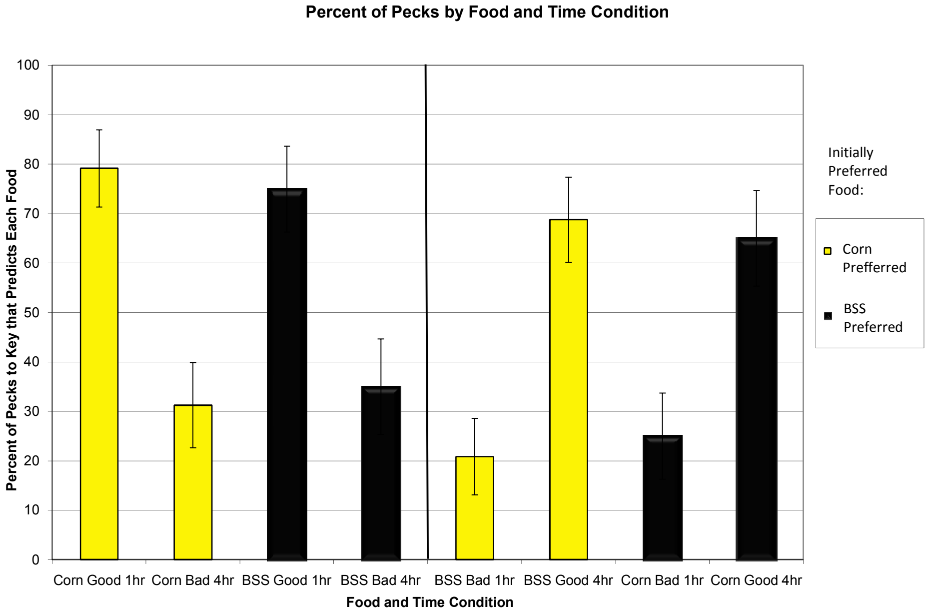

Figure 7. The figure illustrates the percentage of pecking to the keylight that predicted each food outcome, that food's quality, and the time delay. The different colors represent the breakdown of groups by the initially preferred food. During the 4 hour delay, the initially preferred food item has "rotted" and is no longer tasty. During the 1 hour delay, the non-preferred food item is has not yet "ripened" and is not yet tasty. Error bars represent standard error.

With each food item going "bad" at one of the time points, the pigeons showed a dramatic change in pecking behavior based on *when* they last experienced a session with the foods. The pigeons pecked for their initially preferred food item following a short delay at an even higher rate than they showed in baseline testing (77% vs. 62%)

and particularly compared to the levels seen in Experiment 3 (35%). The experience of their non-preferred food item being “bad” at the short delay increased their pecking for their initially preferred food item. In contrast, they showed low levels of pecking for their initially preferred food item when the food had become “rotten” following the long delay (22%) but a strong selection for their initially non-preferred and now ripened food at 4 hours (67%). Thus, the birds seemed to be attending to the “ripening” of their non-preferred food item as well as the “rotting” of their preferred food item.

Experiment 5

The goal of this final experiment was to take the birds’ knowledge of “ripening” and “rotting” food items and attempt to get them to apply this knowledge flexibly to a novel choice situation. The novel choice situation employed was the use of two keylights that the birds had never previously experienced. The birds first experienced the new keylights being paired with the black sunflower seeds and corn, respectively, during the first session of the day, but never experienced the novel keylights being paired with “bad” food items. After experiencing this new relation, the test of the pigeons’ flexibility in using their knowledge about “ripening” and “rotting” was to see how they responded to the new keylights during the second session following either short or long delays. If the birds could flexibly apply their knowledge of food quality changes over time, they should show a change in pecking behavior to the new keylights based on the length of the time delay which previously determined the quality of the food outcome.

Method

In experiment 5, all of the subjects and apparatus are the same as in Experiment 3 and 4. The basic procedure is also the same as in Experiment 4 except as described below.

Procedure

For this experiment, we added two new keylights intermixed with the regular keylights that had been used in Experiments 3 and 4. The new keylights were a white plus or white circle on a dark background. The new keylights and the food outcomes contingent on each were determined randomly and counterbalanced across birds. The first session of the day now included these new stimuli in addition to the red and green lights that were previously used in Experiments 3 and 4. As with the red and green keylights, the circle and plus were presented on each side randomly in 12 trials, were non-reinforced on 4 trials, and were presented together in 2 choice trials. The total number of trials in the first session was increased to 36 trials. The first session continued to occur either 1 or 4 hours prior to the second session of the day. The second session proceeded just as it did in Experiment 4 using only the red and green lights and with red and green keylights each producing one good food item and one bad food item based on the length of delay between sessions. There were no presentations of the new stimuli during this second session. Thus, in the test sessions, the birds had to rely solely on their memory of the relationship between the new keylights and the foods and flexibly apply their knowledge about when each food item either “ripened” or “rotted” to guide their test choices at the given delay. The pigeons experienced on average 8 training days on the new keylights before being tested.

Test sessions consisted of six test trials. The first and last test trial involved the presentation of red and green keylights. The middle four test trials were choice trials between the new keylights: circle and plus. Presentation was counterbalanced so that each stimulus appeared equally on both sides of the chamber. Following these test trials, the session continued with 16 trials presenting only red or green keylights intermixed with the appropriate food outcome as in Experiment 3 and 4. Test sessions were repeated three times for each time delay performed in a counterbalanced order with at least two non-test days between each test day.

Data Analysis

For this experiment, the data were coded in terms of the percent of pecks to the new keylight that predicted the initially preferred food item, which goes bad at the 4 hour delay. Repeated measures ANOVA’s were used to compare the time delay between sessions and the repetition of test sessions as within subjects factors and the preferred food of the birds as a between subjects factor.

Results and Discussion

For this experiment, if the pigeons were showing flexibility in applying their *what-where-when* knowledge, we would expect to see a main effect of the time delay on pecking choices to the novel keylight that predicted their initially preferred food with a high percentage of pecks for short delays when the food is good and a low percentage of pecks for long delays when that food is bad.

The pigeons showed no difference in their pecking to the new keylights based on whether there was a short (M=54.79, SE= 3.95) or long delay (M= 58.96, SE= 5.38) between sessions (F(1, 7)=.486, *ns;* See Figure 8). Likewise, there was no significant difference between replication of test sessions or interactions between the time delay and test sessions (F's<1.4, *ns*). There was also not a significant difference between the groups of birds that were based on their preferred food item or interactions between the initially preferred food group and any other factor (All F's <4.5, *ns*; see Appendix A for breakdown of F values). While the group that preferred black sunflower seeds showed a very slight trend toward pecking the key that predicted black sunflower seeds more when it was good (M=53.33, SE=5.26) than when it was bad (M=45.00, 7.18), the group that preferred corn actually had a fairly strong tendency to peck the new key for corn following the long delay when the corn was bad (M=72.92, SE=8.02) compared to the short delay when it was still good (M=56.25, SE=5.88; See figure 4). This trend is opposite of that expected if they were flexibly applying their knowledge of the temporally based changes in quality to guide their pecking at the new choice keys.

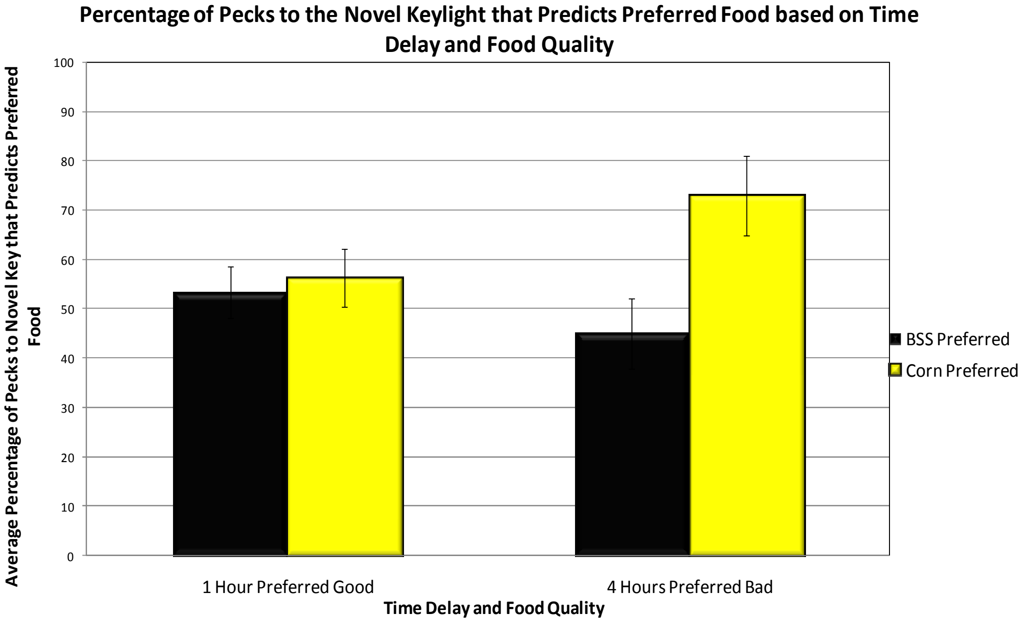

Figure 8. The figure illustrates the percentage of pecking to the new keylight that predicted the initially preferred food outcome based on time delay. The preferred food item is “rotten” at 4 hours, and the non-preferred food item has not yet “ripened” at 1 hour. Error bars represent standard error.

The pigeons did not show any appropriate differentiation between the different time delays when pecking the new keylights. This is in contrast to the pigeons’ actions in Experiment 4 to accurately choose the keylight that predicted the good food outcome at each time delay. The pigeons in Experiment 5 showed no anticipation that the new keylights would produce the same “bad” food item that they had experienced with red and green keylights in their training sessions. Thus, in this experiment, the pigeons failed to show that they could flexibly use their *what-where-when* knowledge in a new situation.

The pigeons in Experiment 5 tended to treat the new keylights as both always producing good food. In fact, this is what the pigeons experienced. They never had direct experience of the new keylights producing bad food. They did not show a generalization of the knowledge of food "rotting" and "ripening" across time and instead treated the new keylights as entirely separate from the totality of events they previously experienced. The lack of flexibility may be due to an inadequacy of the testing methods to detect the pigeons' flexibility. Perhaps, the shift to shape discrimination rather than color discrimination was too difficult for such a brief training period. In support of the difficulty pigeons have in switching stimulus dimensions, Durlach and Mackintosh (1986) found that pigeons can learn to transfer their knowledge about correct choices in a reversal learning task[13] from one set of color stimuli to another different set of colors as discriminative stimuli, but fail to transfer the knowledge between color and orientation of lines. Perhaps if the transfer to new stimuli had been to new color discriminations rather than to new shapes in our experiment, we may have found evidence of flexibility. However, both the increased training and simplification of the stimulus dimensions seem to reduce the extent that the task demonstrates true flexibility of use of the prior *what-where-when* knowledge.

Interestingly, the transfer of reversal learning across stimuli dimensions has been taken as evidence for behavioral flexibility in animals (e.g., see Bond, Kamil, &

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[13] Reversal learning involves the reinforcement of a stimulus to some criterion level and then the immediate change in the stimulus being reinforced.

Balda, 2007). Unlike the pigeons who show little transfer between stimuli of different dimensions, pinyon jays, Clark's nutcrackers, and western scrub jays all show transfer between color discrimination and spatial discrimination in reversal learning tasks (Bond et al., 2007). These findings seem to suggest that corvids show greater behavioral flexibility while pigeons show more rigidity in their behavior. The lack of flexibility in pigeons' *what-where-when* learning is also supported by failures in previous attempts to find flexibility (See Experiment 2).

General Discussion

In our series of experiments, we hypothesized that pigeons could use knowledge of *what, where*, and *when* to guide their foraging choices. Furthermore, we hypothesized that the pigeons could use *what-where-when* knowledge flexibly in a novel choice setting. Pigeons were quite successful at acquiring and using information about *what* food items were available, *where* those food items are accessed, and *when* or how long ago they were last in the experimental chamber which determined whether the food items had "ripened" or "rotted". In Experiment 3, the pigeons decreased their pecking to their preferred food item when that food item had "rotted" following long delays. This was different from their baseline behavior where they showed no distinction between the two time delays. Experiment 4 further demonstrated that pigeons could also use information about foods that "ripen" and are not edible following short delays in addition to continuing to show that they could track the "rotten" food. Unfortunately, the pigeons did not show evidence of flexibility of this knowledge.

There is some ambiguity in the true role that flexibility plays in episodic and episodic-like memory. While it has been considered a feature of episodic memory, it is certainly not unique to episodic memory. Semantic memory is also considered a flexible memory system (see Tulving & Markowitsch, 1998). Furthermore, flexibility may not be necessary to the essence of what episodic memory is but rather may be one feature of the information that is extracted from episodic memories. Finally, Experiment 5 certainly does not preclude pigeons from having flexible memories. It may be that our methods of testing pigeons have just failed to showcase this ability. In fact, we know that pigeons under some circumstances can take knowledge learned in one setting, such as classical conditioning, and apply it in a new setting, such as an operant testing (e.g., Overmier, Ehrman, & Vaughn, 1983) or between operant settings (Zentall et al., 2001).

Even without the evidence of flexibility in the use of *what-where-when* knowledge in pigeons, the present set of experiments tells us a lot about pigeon memory. Pigeons can readily learn to make use of information about how long ago an event occurred to guide their foraging choices. They were even able to use information about both the "ripening" and "rotting" of two different food items over time. Although our methods were similar to those of other episodic-like memory studies, one key difference was the lack of trial-unique stimuli. Without language to communicate the task requirements, working with animals typically necessitates the repetition of stimuli presentations to teach the animals how to respond and what we want them to learn. While few studies have used completely trial unique stimuli, most have used locations that are uniquely marked from trial to trial (e.g., Clayton & Dickinson, 1998; Babb & Crystal, 2005). In our experiments, we used the same stimuli across trials and sessions. Many have argued that the repetition of stimuli produces semantic memories through rule learning (e.g., Clayton et al., 2003; Moscovitch et al., 2006). We have argued previously (see above) that repetition of events may produce semantic memories but does not necessarily eliminate the creation of episodic memories. For example, a person may have had many kisses in their life and know how kisses generally go, but still have an episodic memory of their first kiss. Even if this series of experiments only provides evidence of semantic *what-where-when* knowledge in pigeons, we believe that it is an important step in understanding the nature of episodic-like memory in pigeons. First, Tulving (1985a) believes that episodic memory requires the presence of semantic memory. Thus, a pigeon must have semantic knowledge of *what*, *where,* and *when* if they are to have any hope of showing episodic-like memory. The present experiments are among some of the first to show that pigeons can track different rates of food degradation based on how long ago previous events occurred. This requires the animals to look back to *when* they were previously in the context. It is possible that the pigeons make the judgment about *when* they were last in the context based on relative familiarity, but humans also seem to use this method for judging the occurrence of events (Friedman, 1993).

Although we have an excellent start on understanding episodic-like memory in pigeons, or at the very least *what-where-when* memory, there are still many questions left to be answered. First, it would be useful to create trial unique stimuli for the pigeons to respond to, perhaps by taking advantage of pigeons' perceptual categorization abilities (for review see Khallad, 2004) using a variety of pictures as stimuli. These could be used to train pigeons using a procedure similar to the food "rotting" procedure used in our experiments. Next, pigeons' flexibility should be further tested using a variety of methods. Perhaps by understanding the situations in which pigeons show flexibility in memory and learning tasks, we can better grasp its importance for memory more generally and episodic memory specifically.

Episodic memory in animals is a daunting and difficult topic to study. Each clever experiment that researchers contribute brings us one step closer to understanding the possibility of episodic memory in animals. As we gain knowledge about a variety of species and techniques for studying episodic memory in animals, we also get better and better models for testing human episodic memory functions and deficits. The evidence for episodic memory or at least episodic-like memory in animals is beginning to converge, and we are discovering that humans may not be unique in possessing this powerful memory system.

Chapter 4: General Discussion and Conclusions

The experiments described in this thesis lend support to the idea that animals can show the basic content elements that are necessary for episodic memory. Using methods similar to those of past research (e.g., Clayton & Dickinson, 1998), it has been established that pigeons can show memory of *what* happens, *where* things happen, and *when* things happened. As previously described, pigeons are a useful species in which to expand episodic-like memory studies to because they have a long history of use in studies in psychology and have frequently been used in learning and memory studies (e.g., see Carter & Werner, 1978). Additionally, the use of simple methods, including the use of operant chambers, to test episodic-like memory opens the doors to testing a variety of animal species that may not have caching abilities as part of their behavioral repertoire.

Experiment 1 demonstrated that pigeons could show *what-where-when* memory based on *when* during the day events happened. Specifically, the pigeons were able to track *where* they had to peck in order to get a particular differential food outcome with minimal effort requirements (*what*) based on *when* they were in the session (morning or afternoon). This experiment combined the traditions of time-place learning and episodic-like memory research in order to test whether pigeons could track specific event outcomes based on a time and location dependent availability. This experiment demonstrated that pigeons can form *what-where-when* memories of events based on the time of day.

To further extend the experiments on pigeons toward the research traditions of episodic-like memory, Experiment 3 demonstrated that pigeons could also use *when* in terms of how long ago events occurred while eliminating the use of time of day cues. As in the research of Clayton and Dickinson (1998), the pigeons experienced their preferred food "rotting" by the addition of soap when it had been a relatively long time since they were last in the testing environment. Following short delays, both foods remained good. The pigeons pecked the key that corresponded to their initially preferred foods more following short delays than following long delays (when the food had become "rotten"). Similarly, in Experiment 4, the pigeons showed that they could also learn to alter their pecking to "ripening" foods as well, with their non-preferred food item now "bad" at short delays but "ripening" to "good" food at long delays. This set of experiments was the closest replication to the work of Clayton and Dickinson (1998) performed in pigeons. One aspect that could have made the demonstration more convincing would have been the use of completely trial unique stimuli. In Clayton and Dickinson (1998), as well as in Babb and Crystal (2005, 2006), the location of food items was unique from trial to trial. Because no one has previously demonstrated pigeons' ability to track *what-where-when* over long periods, we decided that the best first step was to attempt to show *what-where-when* memory in situations that were not trial-unique. Certainly, if pigeons could not show *what-where-when* memory in situations with repeated experiences, they would have very little hope of showing *what-where-when* memory of unique experiences. Unfortunately, the repetition of trials has the potential to produce more generic and script-like, semantic memories in humans

(Moscovitch et al., 2006). However, as we have argued previously, this does not necessarily preclude the creation of an episodic memory as well. Even in Clayton and Dickinson (1998), the trial uniqueness did not extend to the entire event, but was limited to the location alone changing from trial to trial with the food items used and the timing of rotting food consistent across trials. In studies of animals, it is typically necessary to repeat trials in order for the animals to learn both what is expected of them and how to make the responses necessary to complete the test. Thus, researchers must find a balance between enough repetitions to allow the animals to learn the task but not so many that they are using semantic memory. In an ideal situation, completely trial unique stimuli should be used to test episodic memory, and in fact, have been used in a few cases (e.g., Ferkin et al., 2008; Dere et al., 2005a; 2006). Even if these memories only constitute the use of semantic *what-where-when* memories, they still provide us with new information on the structure and contents of animal memories. Tulving (1985a; 2002; 2005) argues that episodic memory requires the presence of an intact semantic memory in order to function. Thus, by understanding semantic memory for particular episodes better, we also get closer to understanding episodic memory, *per se.*

One feature that has been used to demonstrate episodic-like memory in animals has been the *flexibility* in use of the memory. Specifically, other researchers have demonstrated that animals can apply their *what-where-when* memory to new situations (e.g., Clayton, Yu, & Dickinson, 2003; Babb & Crystal 2005, 2006). Experiments 2 and 5 of this thesis also attempted to demonstrate the *flexibility* of *what-where-when* memory in pigeons. Unfortunately, however, the pigeons failed to demonstrate *flexibility* in both of these two experiments by failing to apply their knowledge of *what-where-when* to a new situation. Although one cannot use negative results to prove the absence of something, the experiments in this thesis taken together with research from other labs (e.g., Durlach & Mackintosh, 1986) suggests that the behaviors of pigeons may be somewhat more rigid in comparison to other species such as scrub jays (Bond et al., 2007). Alternatively, it is possible that pigeons' behavior is actually more flexible than we realize and that so far we have just failed to find an appropriate way to tap into that *flexibility* for episodic-like memory.

Directions for Future Research

The experiments presented in this thesis provide an excellent start to understanding whether pigeons have the potential for episodic-like memory. There are still, however, many questions left to be answered. First, to create more trial-unique stimuli, pigeons could be trained to peck at a location that contained a picture of some particular category (e.g., chairs or people) as has been done previously (see review in Khallad, 2004). It would also be useful to examine whether pigeons could recognize *who* is involved to help in the creation of trial unique stimuli, particularly since *who* has been proposed as an important element in human episodic memory. These different categories could then be paired with different food outcomes that "rot" or "ripen" over time. By creating trial unique stimuli, the pigeons would be required to use more episodic-like rather than semantic memories to solve the tasks.

Next, pigeons should be further tested on their ability to apply knowledge of *what-where-when* flexibly. By using a variety of manipulations to test *flexibility*, we can begin to understand when pigeons' behavior shows *flexibility* and when they use more rigid representations of events. This expansion of testing *flexibility* should also be extended to the species that have already passed some *flexibility* tests. Specifically, it would be useful to test rats for their flexible behavior given that Babb and Crystal's (2005; 2006) demonstration, as discussed in the first chapter of this thesis, does not convincingly show that rats could apply their knowledge to a new situation.

Finally, it is important to expand testing of episodic memory to a variety of different species to better understand the extent that episodic-like memory is present across the animal kingdom. New forms of testing episodic memory would also be beneficial. Specifically, clever tests that get at the experiential or autonoetic component of episodic memory would lend greater support to the notion of episodic memory in animals, however these are very difficult to conceptualize in a non-verbal animal. As we look for evidence of conscious recollection, we should be cautious that our efforts are not so anthropocentric as to miss the possibility for species specific manifestations of recollective experience.

We also here challenge the human memory researchers to test human amnesiacs on some of the same tests that are being used in animal episodic-like memory tests. If the amnesiac's fail to complete the tasks, the tenet that the animal tests can be solved by semantic memory alone become untenable. Creating non-verbal tests of episodic memory is useful not only in establishing animal models of episodic memory but also in studying the human development of episodic memory in pre-verbal children.

Conclusions

In summary, this thesis has helped to illuminate the presence of *what-where-when* memory in pigeons. Although these demonstrations may fall short of demonstrating full-fledged episodic-like memory because of the repeated nature of the testing, they do provide the groundwork for future demonstrations of episodic-like memory in pigeons. Without the ability to show *what-where-when* memory of repeated events, the search for episodic-like memory of unique events would likely be fruitless[14]. These experiments successfully combined the traditions of time-place learning and episodic-like memory research to show that pigeons can recall events over the course of a day. Furthermore, the experiments have successfully demonstrated that episodic-like memory tests can be adapted to the controlled operant environment. By using operant chambers to run the experiments, the study of episodic-like memory has been opened up to a wide number of variations and species.

The experiments presented in this thesis have implications both for animal researchers and human researchers. First, the testing of pigeons helps to demonstrate that use of *what-where-when* memory is not necessarily a specialized adaptation only for food-storing species such as scrub jays. Instead, the contents (*what-where-when*) of episodic-like memory are likely adaptive and important for a variety of species as

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[14] However, see Graham et al. (2000) for evidence of patients with intact episodic recognition even with impaired semantic memory for that item.

suggested by Gallistel (1990) and Wilkie (1995). As researchers gather more information on a variety of species that exhibit episodic-like memory, we become more convinced that this is not a memory system that is unique to humans, but rather may show widespread occurrence across the animal kingdom.

Second, the expansion of episodic-like memory studies to a highly studied laboratory species using standard laboratory equipment helps to establish the possibility for good animal models of human episodic memory loss. As we gain a better understanding of episodic-like memory functions in animals, we create the potential for more sophisticated models to determine the effectiveness of drug and behavioral treatments for episodic memory loss attributable to damage or disease. Animal models of episodic memory provide the best hope of developing and exploring treatments for people who have lost the ability to reminisce about their past and seem confined to live in a perpetual present. Thus, although experiments of episodic memory in animals are far from easy, the rewards of such efforts certainly make the search worthwhile.

References

Amaral, D. G., & Witter, M. P. (1989). The three dimensional organization of the hippocampal formation: A review of anatomical data. *Neuroscience, 31*, 571-591.

Aragona, B. J., Curtis, J. T., Davidson, A. J., Wang, Z., & Stephan, F. K. (2002). Behavioral and neurochemical investigation of circadian time-place learning in the rat. *Journal of Biological Rhythms, 17*(4), 330-344.

Atance, C., & O'Neill, D. K. (2001). Episodic future thinking. *Trends in Cognitive Sciences, 5*(12), 533-539.

Babb, S. J., & Crystal, J. D. (2005). Discrimination of what, when, and where: Implications for episodic-like memory in rats. *Learning and Motivation, 36*(2), 177-189.

Babb, S. J., & Crystal, J. D. (2006). Episodic-like memory in the rat. *Current Biology, 16*(13), 1317-1321.

Baddeley, A. (2002). The concept of episodic memory. In A. Baddeley, J. P. Aggleton & M. A. Conway (Eds.), *Episodic memory: New directions in research* (pp. 1-10). New York, NY, US: Oxford University Press.

Bauer, P. J. (2007). *Remembering the times of our lives: Memory in infancy and beyond*. Mahwah, NJ: Lawrence Erlbaum Associates Publishers.

Bauer, P. J., Hertsgaard, L. A., & Dow, G. A. (1994). After 8 months have passed: Long-term recall of events by 1- to 2-year-old children. *Memory, 2*(4), 353-382.

Bauer, P. J., Hertsgaard, L. A., & Wewerka, S. S. (1995). Effects of experience and reminding on long-term recall in infancy: Remembering not to forget. *Journal of Experimental Child Psychology, 59*(2), 260-298.

Bauer, P. J., & Mandler, J. M. (1989). One thing follows another: Effects of temporal structure on 1- to 2-year-olds' recall of events. *Developmental Psychology, 25*(2), 197-206.

Bekoff, M. (2002). *Minding animals: Awareness, emotions, and heart*. New York, NY: Oxford University Press.

Biebach, H., Falk, H., & Krebs, J. R. (1991). The effects of constant light and phase shifts on a learned time-place association in garden warblers (sylvia borin): Hourglass or circadian clock? *Journal of Biological Rhythms, 6*(4), 353-365.

Biebach, H., Gordijn, M., & Krebs, J. R. (1989). Time-and-place learning by garden warblers, sylvia borin. *Animal Behaviour, 37*(3), 353-360.

Bird, L. R., Roberts, W. A., Abroms, B., Kit, K. A., & Crupi, C. (2003). Spatial memory for food hidden by rats (Rattus norvegicus) on the radial maze: Studies of memory for where, what, and when. *Journal of Comparative Psychology, 117*(2), 176-187.

Bond, A.B., Kamil, A.C., & Balda, R.P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus, Nucifraga Columbiana, Aphelcoma californica*). *Journal of Comparative Psychology, 121,* 372-379.

Borrini, G., Dall'Ora, P., Della Sala, S., Marinelli, L., & Spinnler, H. (1989). Autobiographical memory. sensitivity to age and education of a standardized enquiry. *Psychological Medicine, 19*(1), 215-224.

Bull, J. A., III, & Overmier, J. B. (1968). Transfer of control of avoidance is not dependent upon the maintenance of the original discriminative response. *Proceedings, 76th Annual Convention, APA*, 143-144.

Burt, C. D. B., Kemp, S., & Conway, M. (2008). Ordering the components of autobiographical events. *Acta Psychologica, 127*(1), 36-45.

Burwell, R., Witter, M., & Amaral, D. (1995). Perirhinal and postrhinal cortices of the rat: A review of the neuroanatomical literature and comparison with findings from the monkey brain. *Hippocampus, 5*(5), 309-408.

Carr, J. A. R., Tan, A. O., & Wilkie, D. M. (1999). Further evidence that rats use ordinal timing in a daily time–place learning task. *Behavioural Processes, 48*(1), 35-48.

Carr, J. A. R., & Wilkie, D. M. (1999). Rats are reluctant to use circadian timing in a daily time–place task. *Behavioural Processes, 44*(3), 287-299.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience, 4*(8), 685-691.

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature, 395*(6699), 272-274.

Clayton, N. S., & Dickinson, A. (1999a). Memory for the content of caches by scrub jays (aphelocoma coerulescens). *Journal of Experimental Psychology: Animal Behavior Processes, 25*(1), 82-91.

Clayton, N. S., & Dickinson, A. (1999b). Motivational control of caching behaviour in the scrub jay, aphelocoma coerulescens. *Animal Behaviour, 57*(2), 435-444.

Clayton, N. S., & Dickinson, A. (1999c). Scrub jays (aphelocoma coerulescens) remember the relative time of caching as well as the location and content of their caches. *Journal of Comparative Psychology (Washington, D.C.: 1983), 113*(4), 403-416.

Clayton, N. S., Emery, N. J., & Dickinson, A. (2006). The prospective cognition of food caching and recovery by western scrub-jays (aphelocoma californica). *Comparative Cognition & Behavior Reviews, 7*(1), 1-11.

Clayton, N. S., Griffiths, D. P., Emery, N. J., & Dickinson, A. (2001). Elements of episodic-like memory in animals. *Philosophical Transactions of the Royal Society of London.Series B, Biological Sciences, 356*(1413), 1483-1491.

Clayton, N. S., Shirley Yu, K., & Dickinson, A. (2003). Interacting cache memories: Evidence for flexible memory use by western scrub-jays (aphelocoma californica). *Journal of Experimental Psychology: Animal Behavior Processes, 29*(1), 14-22.

Clayton, N. S., Yu, K. S., & Dickinson, A. (2001). Scrub jays (aphelocoma coerulescens) form integrated memories of the multiple features of caching episodes. *Journal of Experimental Psychology: Animal Behavior Processes, 27*(1), 17-29.

Cohen, N. J., Poldrack, R. A., & Eichenbaum, H. (1997). Memory for items and memory for relations in the procedural/declarative memory framework. *Memory (Hove, England), 5*(1-2), 131-178.

Conway, M. A. (2002). Sensory-perceptual episodic memory and its context: Autobiographical memory. In A. Baddeley, J. P. Aggleton & M. A. Conway (Eds.), *Episodic memory: New directions in research* (pp. 53-70). New York, NY: Oxford University Press.

Correia, S., Dickinson, A., & Clayton, N. (2007). Western scrub-jays anticipate future needs independently of their current motivational state. *Current Biology, 17*(10), 856-861.

Cowey, A., & Stoerig, P. (1997). Visual detection in monkeys with blindsight. *Neuropsychologia, 35*(7), 929-939.

Cowie, R. J., Krebs, J. R., & Sherry, D. F. (1981). Food storing by marsh tits. *Animal Behaviour, 29*(4), 1252-1259.

Crane, L., & Goddard, L. (2008). Episodic and semantic autobiographical memory in adults with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 38*(3), 498-506.

Crystal, J. D. (2006). Long-interval timing is based on a self-sustaining endogenous oscillator. *Behavioural Processes, 72*(2), 149-160.

Dahl, R. E., & Spear, L. P. (Eds.). (2004). *Adolescent brain development: Vulnerabilities and opportunities.* New York, NY, US: New York Academy of Sciences.

Dallal, N. L., & Meck, W. H. (1990). Hierarchical structures: Chunking by food type facilitates spatial memory. *Journal of Experimental Psychology: Animal Behavior Processes, 16*(1), 69-84.

Dally, J. M., Emery, N. J., & Clayton, N. S. (2006). Food-caching western scrub-jays keep track of who was watching when. *Science, 312*(5780), 1662-1665.

D'Amato, M., & Colombo, M. (1985). Auditory matching-to-sample in monkeys (cebus apella). *Animal Learning & Behavior, 13*(4), 375-382.

Davies, I. R., Sowden, P. T., Jerrett, D. T., Jerrett, T., & Corbett, G. G. (1998). A cross-cultural study of english and setswana speakers on a colour triads task: A test of the sapir-whorf hypothesis. *British Journal of Psychology, 89*(1), 1-15.

de Kort, S. R., Dickinson, A., & Clayton, N. S. (2005). Retrospective cognition by food-caching western scrub-jays. *Learning and Motivation, 36*(2), 159-176.

Della Sala, S., Laiacona, M., Spinnler, H., & Trivelli, C. (1993). Autobiographical recollection and frontal damage. *Neuropsychologia, 31*(8), 823-839.

Denny, M., & Leckart, B. T. (1965). Alternation behavior: Learning and extinction one trial per day. *Journal of Comparative and Physiological Psychology, 60*(2), 229-232.

Dere, E., Huston, J. P., & Souza Silva, M. A. (2005a). Episodic-like memory in mice: Simultaneous assessment of object, place and temporal order memory. *Brain Research Protocols, 16*(1-3), 10-19.

Dere, E., Huston, J. P., & Souza Silva, M. A. (2005b). Integrated memory for objects, places, and temporal order: Evidence for episodic-like memory in mice. *Neurobiology of Learning and Memory, 84*(3), 214-221.

Dere, E., Kart-Teke, E., Huston, J., & De Souza Silva, M. (2006). The case for episodic memory in animals. *Neuroscience & Biobehavioral Reviews, 30*(8), 1206-1224.

Devenport, L., Humphries, T., & Devenport, J. (1998). Future value and patch choice in least chipmunks. *Animal Behaviour, 55*(6), 1571-1581.

Deweer, B., Pillon, B., Pochon, J., & Dubois, B. (2001). Is the HM story only a "remote memory?': Some facts about hippocampus and memory in humans. *Behavioural Brain Research, 127*(1-2), 209-224.

Divac, I., Holst, M. C., Nelson, J., & McKenzie, J. S. (1987). Afferents of the frontal cortex in the echidna (tachyglossus aculeatus). indication of an outstandingly large prefrontal area. *Brain, Behavior and Evolution, 30*(5-6), 303-320.

Durlach, P. J., & Mackintosh, N. J. (1986). Transfer of serial reversal learning in the pigeon. *Quarterly Journal of Experimental Psychology Section B, 38*(1), 81-95.

Eacott, M. J., Easton, A., & Zinkivskay, A. (2005). Recollection in an episodic-like memory task in the rat. *Learning & Memory, 12*(3), 221-223.

Eichenbaum, H., & Fortin, N. J. (2005). Bridging the gap between brain and behavior: Cognitive and neural mechanisms of episodic memory. *Journal of the Experimental Analysis of Behavior, 84*(3), 619-629.

Einstein, G. O., & McDaniel, M. A. (2005). Prospective memory: Multiple retrieval processes. *Current Directions in Psychological Science, 14*(6), 286-290.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., et al. (2003). Cellular networks underlying human spatial navigation. *Nature, 425*(6954), 184-188.

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306*(5703), 1903-1907.

Epstein, R., Lanza, R. P., & Skinner, B. F. (1981). "Self-awareness" in the pigeon. *Science, 212*(4495), 695-696.

Ergorul, C., & Eichenbaum, H. (2004). The hippocampus and memory for "what," "where," and "when". *Learning & Memory, 11*(4), 397-405.

Falk, H., Biebach, H., & Krebs, J. R. (1992). Learning a time-place pattern of food availability: A comparison between an insectivorous and a granivorous weaver species (ploceus bicolor and euplectes hordeaceus). *Behavioral Ecology and Sociobiology, 31*(1), 9-15.

Ferbinteanu, J., Kennedy, P. J., & Shapiro, M. L. (2006). Episodic memory--from brain to mind. *Hippocampus, 16*(9), 691-703.

Ferkin, M. H., Combs, A., del BarcoTrillo, J., Pierce, A. A., & Franklin, S. (2008). Meadow voles, microtus pennsylvanicus, have the capacity to recall the "what", "where", and "when" of a single past event. *Animal Cognition, 11*(1), 147-159.

Fivush, R., Haden, C., & Reese, E. (1996). Remembering, recounting, and reminiscing: The development of autobiographical memory in social context. In D. C. Rubin (Ed.), *Remembering our past: Studies in autobiographical memory* (pp. 341-359). New York, NY: Cambridge University Press.

Foote, A. L., & Crystal, J. D. (2007). Metacognition in the rat. *Current Biology, 17*(6), 551-555.

Fortin, N. J., Agster, K. L., & Eichenbaum, H. B. (2002). Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience, 5*(5), 458-462.

Fortin, N. J., Wright, S. P., & Eichenbaum, H. (2004). Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature, 431*(7005), 188-191.

Friedman, W. J. (1993). Memory for the time of past events. *Psychological Bulletin, 113*(1), 44-66.

Friedman, W. J. (2005). Developmental and cognitive perspectives on humans' sense of the times of past and future events. *Learning and Motivation, 36*(2), 145-158.

Friedman, W.J. (2007). The meaning of "time" in episodic memory and mental time travel. *The Behavioral and Brain Sciences, 30*(3), in discussion 313-51.

Gallistel, C.R. (1990). *The Organization of Learning.* Cambridge, MA: MIT Press.

Gallup Jr, G. (1983). Toward a comparative psychology of mind. In R. L. Mellgren (Ed.), *Animal cognition and behavior* (pp. 473-510). New York, NY: North-Holland.

Gallup, G. G. (1970). Chimpanzees: Self-recognition. *Science, 167*(3914), 86-87.

Gallup, G. G. (1982). Self-awareness and the emergence of mind in primates. *American Journal of Primatology, 2*(3), 237-248.

Gardiner, J. M. (1988). Functional aspects of recollective experience. *Memory & Cognition, 16*(4), 309-313.

Gathercole, S. E. (1998). The development of memory. *Journal of Child Psychology and Psychiatry, 39*(1), 3-27.

Goodall, J. (1986). *The chimpanzees of gombe: Patterns of behavior*. Cambridge, MA: Belknap Press of Harvard University Press.

Graham, K. S., Simons, J. S., Pratt, K. H., Patterson, K., & Hodges, J. R. (2000). Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia, 38*(3), 313-324.

Grant, D. S., & Roberts, W. A. (1973). Trace interaction in pigeon short-term memory. *Journal of Experimental Psychology, 101*(1), 21-29.

Greenfield, P., & Savage-Rumbaugh, S. (1990). Grammatical combination in pan paniscus: Process of learning and invention in the evolution and development of language. In S. T. Parker, & K. R. Gibson (Eds.), *Language and intelligence in monkeys and apes* (pp. 540-578). Cambridge, MA: Cambridge University Press.

Hampton, R. R. (2001). Rhesus monkeys know when they remember. *Proceedings of the National Academy of Sciences USA, 98*(9), 5359-5362.

Hampton, R. R., Hampstead, B. M., & Murray, E. A. (2005). Rhesus monkeys (macaca mulatta) demonstrate robust memory for what and where, but not when, in an open-field test of memory. *Learning and Motivation, 36*(2), 245-259.

Hampton, R. R., & Schwartz, B. L. (2004). Episodic memory in nonhumans: What, and where, is when? *Current Opinion in Neurobiology, 14*(2), 192-197.

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 104*(5), 1726-1731.

Hauser, M. D., Kralik, J., Botto-Mahan, C., Garrett, M., & Oser, J. (1995). Self-recognition in primates: Phylogeny and the salience of species-typical features. *Proceedings of the National Academy of Sciences of the United States of America, 92*(23), 10811-10814.

Healy, A. F., Cunningham, T. F., Shea, K. M., & Kole, J. A. (2007). The effects of familiarity on reconstructing the order of information in semantic and episodic memory. In J. S. E. Nairne (Ed.), *The foundations of remembering: Essays in honor of henry L. roediger, III.* (pp. 191-208). New York, NY: Psychology Press.

Heyes, C. M. (1998). Theory of mind in nonhuman primates. *The Behavioral and Brain Sciences, 21*(1), 101-14; discussion 115-48.

Holland, P., C., & Rescorla, R. A. (1975). The effect of two ways of devaluing the unconditioned stimulus after first- and second-order appetitive conditioning. *Journal of Experimental Psychology: Animal Behavior Processes, 1*(4), 355-363.

Jacobs, L. F. (1992). Memory for cache locations in merriam's kangaroo rats. *Animal Behaviour, 43*(4), 585-593.

KartTeke, E., Souza Silva, M. A., Huston, J. P., & Dere, E. (2006). Wistar rats show episodic-like memory for unique experiences. *Neurobiology of Learning and Memory, 85*(2), 173-182.

Khallad, Y. (2004). Conceptualization in the pigeon: What do we know? *International Journal of*

Psychology, 39(2), 73-94.

Killeen, P. R. (1978). Superstition: A matter of bias, not detectability. *Science, 199*(4324), 88-90.

Killeen, P. R., & Smith, J. P. (1984). Perception of contingency in conditioning: Scalar timing, response bias, and erasure of memory by reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes, 10*(3), 333-345.

Klein, S., Chan, R., & Loftus, J. (1999). Independence of episodic and semantic self-knowledge: The case from autism. *Social Cognition, 17*(4), 413-436.

Kopelman, M., Wilson, B., & Baddeley, A. (1989). The autobiographical memory interview: A new assessment of autobiographical and personal semantic memory in amnesiac patients. *Journal of Clinical and Experimental Neuropsychology, 11*(5), 724-744.

Krebs, J. R. (1990). Food-storing birds: Adaptive specialization in brain and behaviour? *Philosophical Transactions: Biological Sciences, 329*(1253), 153-160.

Krebs, J. R., Healy, S. D., & Shettleworth, S. J. (1990). Spatial memory of paridae: Comparison of a storing and a non-storing species, the coal tit, parus ater, and the great tit, P. major. *Animal Behaviour, 39*(6), 1127-1137.

Loftus, E. F. (1993). Desperately seeking memories of the first few years of childhood: The reality of early memories. *Journal of Experimental Psychology: General, 122*(2), 274-277.

Lubinski, D., & Thompson, T. (1987). An animal model of the interpersonal communication of interoceptive (private) states. *Journal of the Experimental Analysis of Behavior, 48*(1), 1-15.

Lubinski, D., & Thompson, T. (1993). Species and individual differences in communication based on private states. *Behavioral and Brain Sciences, 16*(4), 627-680.

Lukoyanov, N. V., Pereira, P. A., Mesquita, R. M., & Andrade, J. P. (2002). Restricted feeding facilitates time-place learning in adult rats. *Behavioural Brain Research, 134*(1-2), 283-290.

Manrique, T., Molero, A., Ballesteros, M. A., Moron, I., Gallo, M., & Fenton, A. A. (2004). Time of day-dependent latent inhibition of conditioned taste aversions in rats. *Neurobiology of Learning and Memory, 82*(2), 77-80.

Mather, M., Henkel, L. A., & Johnson, M. K. (1997). Evaluating characteristics of false memories: Remember/know judgments and memory characteristics questionnaire compared. *Memory & Cognition, 25*(6), 826-837.

Mayes, A. R., & Roberts, N. (2002). Theories of episodic memory. In A. Baddeley, J. P. Aggleton & M. A. Conway (Eds.), *Episodic memory: New directions in research.* (pp. 86-109). New York, NY: Oxford University Press.

Mazur, J. E., & Logue, A. (1978). Choice in a self-control paradigm: Effects of a fading procedure. *Journal of the Experimental Analysis of Behavior, 30*(1), 11-17.

McCormack, T., & Hoerl, C. (1999). Memory and temporal perspective: The role of temporal frameworks in memory development. *Developmental Review, 19*(1), 154-182.

McDonald, R.J., Hong, N.S., Ray, C., & Ralph, M.R. (2002). No time of day modulation or time stamp on multiple memory tasks in rats. *Learning and Motivation, 33,* 230-252.

McDonough, L., Mandler, J. M., McKee, R. D., & Squire, L. R. (1995). The deferred imitation task as a nonverbal measure of declarative memory. *Proceedings of the National Academy of Sciences of the United States of America, 92*(16), 7580-7584.

McKenzie, T., Bird, L. R., & Roberts, W. A. (2005). The effects of cache modification on food caching and retrieval behavior by rats. *Learning and Motivation, 36* (2), 260-278.

McKenzie, T., Cherman, T., Bird, L. R., Naqshbandi, M., & Roberts, W. A. (2004). Can squirrel monkeys (saimiri sciureus) plan for the future? studies of temporal myopia in food choice. *Learning & Behavior, 32*(4), 377-390.

Meltzoff, A. N. (1988). Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Developmental Psychology, 24*(4), 470-476.

Menzel, C. R. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (pan troglodytes) after extended delays. *Journal of Comparative Psychology, 113*(4), 426-434.

Mercado, E., Murray, S. O., Uyeyama, R. K., Pack, A. A., & Herman, L.M. (1998). Memory for recent actions in the bottlenosed dolphin (Tursiops truncatus): Repetition of arbitrary behaviors using an abstract rule. *Animal Learning & Behavior, 26*, 210-218.

Metcalfe, J., Cottrell, G. W., & Mencl, W. E. (1992). Cognitive binding: A computational-modeling analysis of a distinction between implicit and explicit memory. *Journal of Cognitive Neuroscience, 4*(3), 289-298.

Milner, B., Corsi, P., & Leonard, G. (1991). Frontal-lobe contribution to recency judgments. *Neuropsychologia, 29*(6), 601-618.

Monk, C. S., Zhuang, J., Curtis, W. J., Ofenloch, I., Tottenham, N., Nelson, C. A., et al. (2002). Human hippocampal activation in the delayed matching-and nonmatching-to-sample memory tasks: An event-related functional MRI approach. *Behavioral Neuroscience, 116*(4), 716-721.

Moron, I., Manrique, T., Molero, A., Ballesteros, M. A., Gallo, M., & Fenton, A. (2002). The contextual modulation of conditioned taste aversions by the physical environment and time of day is similar. *Learning & Memory, 9*(5), 218-223.

Morris, R. G. (2001). Episodic-like memory in animals: Psychological criteria, neural mechanisms and the value of episodic-like tasks to investigate animal models of neurodegenerative disease. *Philosophical Transactions of the Royal Society of London - Series B: Biological Sciences, 356*(1413), 1453-65,.

Moscovitch, M., Nadel, L., Winocur, G., Gilboa, A., & Rosenbaum, R. (2006). The cognitive neuroscience of remote episodic, semantic and spatial memory. *Current Opinion in Neurobiology, 16*(2), 179-190.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., et al. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. *Journal of Anatomy, 207*(1), 35-66.

Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science, 312*(5776), 1038-1040.

Naqshbandi, M., Feeney, M. C., McKenzie, T. L., & Roberts, W. A. (2007). Testing for episodic-like memory in rats in the absence of time of day cues: Replication of Babb and crystal. *Behavioural Processes, 74*(2), 217-225.

Neisser, U. (1982). *Memory observed: Remembering in natural contexts*. San Francisco: WH Freeman.

Nelson, K. (1993). The psychological and social origins of autobiographical memory. *Psychological Science, 4*(1), 7-14.

Northcutt, R. G. (1981). Evolution of the telencephalon in nonmammals. *Annual Review of Neuroscience, 4*, 301-350.

Nyberg, L., & Tulving, E. (1996). Classifying human long-term memory: Evidence from converging dissociations. *European Journal of Cognitive Psychology, 8*(2), 163-183.

Okado, Y., & Stark, C. E. (2005). Neural activity during encoding predicts false memories created by misinformation. *Learning & Memory, 12*(1), 3-11.

Olton, D. S. (1979). Mazes, maps, and memory. *American Psychologist, 34*(7), 583-596.

Overmier, J. B., Ehrman, R. N., & Vaughn, J. C. (1983). Pavlovian processes do mediate control of the "avoidance" response strategy. *Learning and Motivation, 14*, 182-203.

Overmier, J. B., & Leaf, R. C. (1965). Effects of discriminative Pavlovian fear conditioning upon previously or subsequently acquired avoidance responding. *Journal of Comparative and Physiological Psychology, 60(2),* 213-217.

Perfect, T., Mayes, A., Downes, J., & Van Eijk, R. (1996). Does context discriminate recollection from familiarity in recognition memory? *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology, 49*(3), 797-813.

Perner, J., & Ruffman, T. (1995). Episodic memory an autonoetic consciousness: Developmental evidence and a theory of childhood amnesia. *Journal of Experimental Child Psychology, 59*(3), 516-548.

Petruso, E. J., Fuchs, T., & Bingman, V. P. (2007). Time-space learning in homing pigeons (*columba livia*): Orientation to an artificial light source. *Animal Cognition, 10*(2), 181-188.

Pillemer, D. B., Picariello, M. L., & Pruett, J. C. (1994). Very long-term memories of a salient preschool event. *Applied Cognitive Psychology, 8*(2), 95-106.

Pizzo, M.J., & Crystal, J.D. (2004). Time-place learning in the eight-arm radial maze.

Learning & Behavior, 32, 240-255.

Plotnik, J. M., de Waal, F. B. M., & Reiss, D. (2006). Self-recognition in an Asian elephant. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 103*(45), 17053-17057.

Posada, S., & Colell, M. (2007). Another gorilla (gorilla gorilla gorilla) recognizes himself in a mirror. *American Journal of Primatology, 69*(5), 576-583.

Povinelli, D. J., Bering, J. M., & Giambrone, S. (2000). Toward a science of other minds: Escaping the argument by analogy. *Cognitive Science: A Multidisciplinary Journal, 24*(3), 509-541.

Povinelli, D. J., Theall, L. A., Reaux, J. E., & DunphyLelii, S. (2003). Chimpanzees spontaneously alter the location of their gestures to match the attentional orientation of others. *Animal Behaviour, 66*(1), 71-79.

Pravosudov, V. V., & de Kort, S. R. (2006). Is the western scrub-jay (aphelocoma californica) really an underdog among food-caching corvids when it comes to hippocampal volume and food caching propensity? *Brain, Behavior and Evolution, 67*(1), 1-9.

Prior, H., Schwarz, A., & Gunturkun, O. (2008). Mirror-induced behavior in the magpie (pica pica): Evidence of self-recognition. *PLoS Biology, 6*(8), e202.

Raby, C., Alexis, D., Dickinson, A., & Clayton, N. (2007). Planning for the future by western scrub-jays. *Nature, 445*(7130), 919-921.

Reeve, H. K., & Sherman, P. W. (1993). Adaptation and the goals of evolutionary research. *The Quarterly Review of Biology, 68*(1), 1-32.

Reichman, W.E., & Negro, A. (2001). Negative symptoms in the elderly patient with dementia. *International Journal of Geriatric Psychiatry, 16,* S7-S11.

Reiss, D., & Marino, L. (2001). Mirror self-recognition in the bottlenose dolphin: A case of cognitive convergence. *Proceedings of the National Academy of Sciences of the United States of America, 98*(10), 5937-5942.

Rescorla, R. A. (1992). Depression of an instrumental response by a single devaluation of its outcome. *The Quarterly Journal of Experimental Psychology B: Comparative and Physiological Psychology, 44B*(2), 123-136.

Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin, 128*(3), 473-489.

Rodriguez, F., Lopez, J., Vargas, J., Broglio, C., Gomez, Y., & Salas, C. (2002). Spatial memory and hippocampal pallium through vertebrate evolution: Insights from reptiles and teleost fish. *Brain Research Bulletin, 57*(3-4), 499-505.

Roediger, H. L.,III. (1996). Commentary: Prospective memory and episodic memory. In M. Brandimonte, G. O. Einstein & M. A. McDaniel (Eds.), *Prospective memory: Theory and applications.* (pp. 149-155). Mahwah, NJ: Lawrence Erlbaum Associates Publishers.

Rubin, D. C. (1982). On the retention function for autobiographical memory. *Journal of Verbal Learning & Verbal Behavior, 21*(1), 21-38.

Saksida, L. M., & Wilkie, D. M. (1994). Time-of-day discrimination by pigeons, columba livia. *Animal Learning & Behavior, 22*(2), 143-154.

Schacter, D. L. (1999). The seven sins of memory: Insights from psychology and cognitive neuroscience. *American Psychologist, 54*(3), 182-203.

Schacter, D. L., Harbluk, J. L., & McLachlan, D. R. (1984). Retrieval without recollection: An experimental analysis of source amnesia. *Journal of Verbal Learning & Verbal Behavior, 23*(5), 592-611.

Schacter, D. L., Kaszniak, A. W., Kihlstrom, J. F., & Valdiserri, M. (1991). The relation between source memory and aging. *Psychology and Aging, 6*(4), 559-568.

Schwartz, B. L., Colon, M. R., Sanchez, I. C., Rodriguez, I. A., & Evans, S. (2002). Single-trial learning of "what" and "who" information in a gorilla (gorilla gorilla gorilla): Implications for episodic memory. *Animal Cognition, 5*(2), 85-90.

Schwartz, B. L., & Evans, S. (2001). Episodic memory in primates. *American Journal of Primatology, 55*(2), 71-85.

Schwartz, B. L., Hoffman, M. L., & Evans, S. (2005). Episodic-like memory in a gorilla: A review and new findings. *Learning and Motivation, 36*(2), 226-244.

Sherry, D., Jacobs, L., & Gaulin, S. (1992). Spatial memory and adaptive specialization of the hippocampus. *Trends Neuroscience, 15*(8), 298-303.

Sherry, D.F., Forbes, M.R.L., Khurgel, M, & Ivy, G.O. (1993). Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird. *Proceedings of the National Academy of Science, 90*, 7839-7843.

Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review, 94*(4), 439-454.

Shimamura, A. P., Janowsky, J. S., & Squire, L. R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia, 28*(8), 803-813.

Shimp, C. P. (1982). On meta-knowledge in the pigeon: An organism's knowledge about its own behavior. *Animal Learning & Behavior, 10*(3), 358-364.

Silberberg, A., Widholm, J. J., Bresler, D., Fujito, K., & Anderson, J. R. (1998). Natural choice in nonhuman primates. *Journal of Experimental Psychology: Animal Behavior Processes, 24*(2), 215-228.

Singer, R. A., & Zentall, T. R. (2007). Pigeons learn to answer the question "where did you just peck?" and can report peck location when unexpectedly asked. *Learning & Behavior, 35*(3), 184-189.

Skov-Rackette, S. I., Miller, N. Y., & Shettleworth, S. J. (2006). What-where-when memory in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 32*(4), 345-358.

Small, W. S. (1901). Experimental study of the mental process of the rat. II. *American Journal of Psychology, 12*(2), 206-239.

Smith, J., Shields, W. E., & Washburn, D. A. (2003). The comparative psychology of uncertainty monitoring and metacognition. *Behavioral and Brain Sciences, 26*(3), 317-373.

Smith, J. D., Shields, W. E., Allendoerfer, K. R., & Washburn, D. A. (1998). Memory monitoring by animals and humans, , *Journal of Experimental Psychology: General, 127*(3), 227-250.

Sole, L., Shettleworth, S., & Bennett, P. (2003). Uncertainty in pigeons. *Psychonomic Bulletin & Review, 10*(3), 738-745.

Sperling, G. (1960). The information available in brief visual presentation. *Psychological Monographs, 74*(11), 1-29.

Squire, L. R. (1992). Declarative and nondeclarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience, 4*(3), 232-243.

Squire, L.R., & Zola, S. M. (1998). Episodic memory, semantic memory, and amnesia. *Hippocampus, 8,* 205-211.

Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *The Behavioral and Brain Sciences, 30*(3), 299-313; discussion 313-51.

Suddendorf, T., & Whiten, A. (2001). Mental evolution and development: Evidence for secondary representation in children, great ages, and other animals. *Psychological Bulletin, 127*(5), 629-650.

Suddendorf, T., & Busby, J. (2005). Making decisions with the future in mind: Developmental and comparative identification of mental time travel. *Learning and Motivation, 36*(2), 110-125.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs, 123*(2), 133-167.

Suddendorf, T., & Corballis, M. C. (2008). New evidence for animal foresight? *Animal Behaviour, 75*(5), e1-e3.

Surridge, C., & Amsel, A. (1965). Performance under a single alternation schedule of reinforcement at 24-hour intertrial intervals. *Psychonomic Science, 3*(3), 131-132.

Sutton, J. (2002). Cognitive conceptions of language and the development of autobiographical memory. *Language & Communication, 22*(3), 375-390.

Takahashi, L. K., & Lore, R. K. (1980). Foraging and food hoarding of wild rattus norvegicus in an urban environment. *Behavioral & Neural Biology, 29*(4), 527-531.

Thorpe, C. M., Bates, M. E., & Wilkie, D. M. (2003). Rats have trouble associating all three parts of the time-place-event memory code. *Behavioural Processes, 63*(2), 95-110.

Thorpe, C. M., & Wilkie, D. M. (2007). Rats acquire a low-response-cost daily time-place task with differential amounts of food. *Learning & Behavior, 35*(1), 71-78.

Tinklepaugh, O. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology, 8*(3), 197-236.

Tinklepaugh, O. (1932). The multiple delayed reaction with chimpanzees and monkeys. *Journal of Comparative Psychology, 13*(2), 207-243.

Tobin, H., Chelonis, J. J., & Logue, A. (1993). Choice in self-control paradigms using rats. *Psychological Record, 43*(3), 441-453.

Tobin, H., Logue, A., Chelonis, J. J., & Ackerman, K. T. (1996). Self-control in the monkey macaca fascicularis. *Animal Learning & Behavior, 24*(2), 168-174.

Toda, K., & Watanabe, S. (2008). Discrimination of moving video images of self by pigeons (columba livia). *Animal Cognition, 11*(4), 699-705.

Tulving, E. (1972). Episodic and semantic memory. In E. Tulving, & W. Donaldson (Eds.), *Organisation of memory* (pp. 381-403). San Diego: Academic Press.

Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.

Tulving, E. (1985a). How many memory systems are there? *American Psychologist, 40*(4), 385-398.

Tulving, E. (1985b). Memory and consciousness. *Canadian Psychology Psychologie Canadienne, 26*(1), 1-12.

Tulving, E. (1993). What is episodic memory? *Current Directions in Psychological Science, 2*(3), 67-70.

Tulving, E. (2002). Episodic memory and common sense: How far apart? In A. Baddeley, J. P. Aggleton & M. A. Conway (Eds.), *Episodic memory: New directions in research.* (pp. 269-287). New York, NY: Oxford University Press.

Tulving, E. (2005). Episodic memory and autonoesis: Uniquely human? In H. S. Terrace, & J. Metcalfe (Eds.), *The missing link in cognition: Origins of self-reflective consciousness.* (pp. 3-56). New York, NY: Oxford University Press.

Tulving, E., & Lepage, M. (2000). Where in the brain is the awareness of one's past? [references]. In D. L. Schacter, & E. Scarry (Eds.), *Memory, brain, and belief* (pp. 208-228). Cambridge, MA: Harvard University Press.

Tulving, E., & Markowitsch, H. J. (1998). Episodic and declarative memory: Role of the hippocampus. *Hippocampus, 8*(3), 198-204.

Usher, J. A., & Neisser, U. (1993). Childhood amnesia and the beginnings of memory for four early life events. *Journal of Experimental Psychology: General, 122*(2), 155-165.

Vander Wall, S. B. (1982). An experimental analysis of cache recovery in clark's nutcracker. *Animal Behaviour, 30*(1), 84-94.

Vander Wall, S. B., & Hutchins, H. E. (1983). Dependence of clark's nutcracker (nucifraga columbiana) on conifer seeds during the postfledgling period. *Canadian Field Naturalist, 97*, 89-111.

Vargha-Khadem, F., Gadian, D., Watkins, K., & Connelly, A. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science, 277*(5324), 376-380.

von Fersen, L., & Delius, J. D. (1989). Long-term retention of many visual patterns by pigeons. *Ethology Formerly Zeitschrift Fur Tierpsychologie, 82*(2), 141-155.

Wagenaar, W. A. (1986). My memory: A study of autobiographical memory over six years. *Cognitive Psychology, 18*(2), 225-252.

Wenger, D., Biebach, H., & Krebs, J. R. (1991). Free-running circadian rhythm of a learned

feeding pattern in starlings. *Naturwissenschaften, 78*, 87-89.

Widman, D. R., Gordon, D., & Timberlake, W. (2000). Response cost and time-place discrimination by rats in maze tasks. *Animal Learning & Behavior, 28*(3), 298-309.

Wilkie, D. M. (1995). Time-place learning. *Current Directions in Psychological Science, 4*(3), 85-89.

Williams, D. A., Butler, M. M., & Overmier, J. (1990). Expectancies of reinforcer location and quality as cues for a conditional discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 16*(1), 3-13.

Winocur, G. (1991). Functional dissociation of the hippocampus and prefrontal cortex in learning and memory. *Psychobiology, 19*(1), 11-20.

Wirth, S., Yanike, M., Frank, L. M., Smith, A. C., Brown, E. N., & Suzuki, W. A. (2003). Single neurons in the monkey hippocampus and learning of new associations. *Science, 300*(5625), 1578-1581.

Wood, E. R., Dudchenko, P. A., & Eichenbaum, H. (1999). The global record of memory in hippocampal neuronal activity. *Nature, 397*(6720), 613-616.

Yanike, M., Wirth, S., & Suzuki, W. A. (2004). Representation of well-learned information in the monkey hippocampus. *Neuron, 42*(3), 477-487.

Yonelinas, A. (2001). Components of episodic memory: The contribution of recollection and familiarity. *Philosophical Transactions of the Royal Society B: Biological Sciences, 356*(1413), 1363-1374.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language, 46*(3), 441-517.

Zentall, T. R. (2006). Mental time travel in animals: A challenging question. *Behavioural Processes, 72*(2), 173-183.

Zentall, T. R., Clement, T. S., Bhatt, R. S., & Allen, J. (2001). Episodic-like memory in pigeons. *Psychonomic Bulletin & Review, 8*(4), 685-690.

Zinkivskay, A., Nazir, F., & Smulders, T. V. (2009). *What – where – when* memory in magpies (*pica pica*). *Animal Cognition, 12*(1), 119-125.

Zola, S. M., Squire, L. R., Teng, E., Stefanacci, L., Buffalo, E. A., & Clark, R. E. (2000). Impaired recognition memory in monkeys after damage limited to the hippocampal region. *Journal of Neuroscience, 20*(1), 451-463.

Appendix A

Experiment 1: ANOVA Table- AM/PM					
Variable	SS	df	MS	F	Sig
Time of Day	5062.5	1	5062.5	5.65	0.041
Error (Time)	8062.5	9	895.833		
Order	62.5	1	62.5	0.04	0.84
Error (Order)	13062.5	9	1451.389		
Time*Order	62.5	1	62.5	0.1	0.758
Error(Time*Order)	5562.5	9	618.056		

Experiment 2: ANOVA Table-Flexibility(Tone_Buzz)					
Variable	SS	df	MS	F	Sig
Time of Day	24500	1	24500	15.31	0.004
Error (Time)	14406.25	9	1600.69		
Order	2531.25	1	2531.25	5.44	0.045
Error (Order)	4187.5	9	465.28		
Time*Order	500	1	500	0.38	0.553
Error(Time*Order)	11843.75	9	1315.97		
Tone_Buzz	125	1	125	0.88	0.373
Error (Tone_Buzz)	1281.25	9	142.36		
Time*Tone_Buzz	31.25	1	31.25	0.06	0.808
Error(Time*Tone)	4500	9	500		
Order*Tone_Buzz	500	1	500	1.21	0.3
Error(Order*Tone)	3718.75	9	413.194		
Time*Order*Tone	281.25	1	281.25	0.49	0.502
Error(Time*Order*Tone)	5187.5	9	576.389		

Experiment 3a: ANOVA Table- Baseline					
Variable	SS	df	MS	F	Sig
Session	86.81	1	86.81	0.6	0.465
Session*Preferred Food	420.14	1	420.14	2.89	0.133
Error(Session)	1018.75	7	145.54		
Time_between	281.25	1	281.25	2.03	0.197
Time_between*Preferred	281.25	1	281.25	2.03	0.197
Error(Time_between)	968.75	7	138.39		
Session*Time_between	190.14	1	190.14	2.05	0.195
Session*Time*Preferred	390.14	1	390.14	4.21	0.079
Error(Session*Time*Pref)	648.75	7	92.68		
Foodbad	361.25	1	361.25	0.88	0.381
Error(Foodbad)	2888.75	7	412.68		

Experiment 3b: ANOVA Table- 4hr Rotten					
Variable	SS	df	MS	F	Sig
Session	995.66	2	497.83	1.84	0.195
Session*Preferred Food	370.66	2	185.33	0.69	0.519
Error(Session)	3778.65	14	269.9		
Time_between	3000	1	3000	19.77	0.003
Time_between*Preferred	37.04	1	37.04	0.244	0.636
Error(Time_between)	1062.5	7	151.79		
Session*Time_between	745.66	2	372.83	1.1	0.361
Session*Time*Preferred	305.845	2	152.92	0.45	0.647
Error(Session*Time)	4757.81	14	339.84		
Foodbad	5333.33	1	5333.33	3.74	0.094
Error(Foodbad)	9979.17	7	1425.6		

Experiment 4: ANOVA Table- 1hr Ripen /4hr Rotten					
Variable	SS	df	MS	F	Sig
Session	1177.37	2	588.69	4.8	0.026
Session*Preferred Food	66.26	2	33.13	0.27	0.767
Error(Session)	1716.15	14	122.58		
Time_between	25764.47	1	125764.5	29.32	0.001
Time_between*Preferred	208.91	1	208.91	0.24	0.641
Error(Time_between)	6151.04	7	878.72		
Session*Time_between	599.25	2	299.62	1.83	0.197
Session*Time*Preferred	43.69	2	21.85	0.13	0.876
Error(Session*Time)	2294.27	14	163.88		
Foodbad	0.58	1	0.58	0.001	0.983
Error(Foodbad)	8026.04	7	1146.58		

Experiment 5: ANOVA Table- Flexibility					
Variable	SS	df	MS	F	Sig
Session	1166.67	2	583.33	0.86	0.443
Session*Preferred Food	240.74	2	120.37	0.18	0.839
Error(Session)	9458.33	14	675.6		
Time_between	231.48	1	231.48	0.49	0.508
Time_between*Preferred	2083.33	1	2083.33	4.38	0.075
Error(Time_between)	3333.33	7	476.19		
Session*Time_between	1462.96	2	731.48	1.35	0.289
Session*Time*Preferred	166.67	2	83.33	0.16	0.858
Error(Session*Time)	7541.67	14	538.69		
Foodbad	3168.98	1	3168.98	4.5	0.073
Error(Foodbad)	4979.17	7	711.31		

Appendix B

Experiment 1: Raw Data - AM/PM and Order- DV: Percent of pecks to Optimal Morning Key

	AM		PM	
Bird	1st	2nd	1st	2nd
251	100	100	0	50
102	0	100	0	50
103	0	0	0	0
104	0	0	0	0
105	100	100	50	50
107	100	100	50	100
108	100	50	100	50
109	100	0	0	0
110	0	0	50	0
112	50	100	50	50

Experiment 2: Raw Data - AM/PM, Order, and Auditory Cue- DV: Percent of pecks to Optimal Morning Key

	AM				PM			
	1st		2nd		2nd		1st	
Bird	Tone	Buzz	Tone	Buzz	Tone	Buzz	Tone	Buzz
251	75	25	75	75	0	50	50	50
102	100	50	100	100	0	0	0	50
103	0	0	0	0	0	0	0	0
104	100	50	50	100	0	0	50	50
105	100	100	50	50	25	25	25	0
107	100	100	50	100	100	100	100	100
108	50	75	50	100	75	25	25	50
109	100	50	0	0	0	0	0	0
110	50	25	25	25	100	75	25	25
112	50	0	0	25	100	100	75	75

Experiment 3a: Raw Data - Baseline: test session and time delay- DV: Percent of Pecks to Key for Preferred Food					
		Test 1		Test 2	
Bird	Preference	1hr	4hr	1hr	4hr
102	Corn	60	70	60	60
103	BSS	50	80	80	80
104	BSS	60	60	50	60
105	BSS	50	50	70	60
107	BSS	50	40	50	40
108	Corn	80	40	40	40
109	Corn	80	60	70	80
110	BSS	50	40	70	70
112	Corn	90	50	80	70

Experiment 3a: Raw Data - 4hr Rotten: test session and time delay- DV: Percent of Pecks to Key for Preferred Food							
		Test 1		Test 2		Test 3	
Bird	Preference	1hr	4hr	1hr	4hr	1hr	4hr
102	Corn	100	62.5	37.5	75	62.5	50
103	BSS	37.5	0	25	37.5	37.5	25
104	BSS	0	0	12.5	12.5	0	12.5
105	BSS	25	0	12.5	12.5	37.5	12.5
107	BSS	37.5	37.5	25	0	25	0
108	Corn	37.5	50	50	0	87.5	50
109	Corn	25	25	25	0	37.5	12.5
110	BSS	12.5	12.5	12.5	0	62.5	0
112	Corn	12.5	25	37.5	0	37.5	0

Experiment 4: Raw Data - 1hr Ripen & 4hr Rotten: test session and time delay- DV: Percent of Pecks to Key for Preferred Food							
		Test 1		Test 2		Test 3	
Bird	Preference	1hr	4hr	1hr	4hr	1hr	4hr
102	Corn	75	62.5	37.5	62.5	62.5	37.5
103	BSS	50	12.5	50	12.5	37.5	0
104	BSS	75	37.5	62.5	37.5	87.5	25
105	BSS	75	62.5	75	62.5	62.5	50
107	BSS	87.5	37.5	75	12.5	100	25
108	Corn	75	37.5	62.5	25	100	0
109	Corn	87.5	12.5	100	25	75	0
110	BSS	100	62.5	100	50	87.5	37.5
112	Corn	100	50	100	25	75	37.5

Experiment 5: Raw Data - 1hr Ripen & 4hr Rotten: test session and time delay- DV: Percent of Pecks to New Key for Preferred Food							
		Test 1		Test 2		Test 3	
Bird	Preference	1hr	4hr	1hr	4hr	1hr	4hr
102	Corn	50	75	25	75	50	75
103	BSS	50	25	50	25	50	25
104	BSS	50	25	50	25	25	75
105	BSS	50	50	75	50	75	100
107	BSS	75	50	50	75	0	25
108	Corn	75	75	75	75	50	75
109	Corn	25	75	100	100	50	100
110	BSS	50	25	75	75	75	25
112	Corn	75	0	25	75	75	75