Published in final edited form as:

Behav Brain Res. 2010 December 31; 215(2): 235–243. doi:10.1016/j.bbr.2010.03.005.

Episodic-like memory in animals

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Abstract

Episodic memory consists of representations of unique past events. It has been argued that episodic memory is grounded in a temporal framework, meaning that we remember when an event occurred. The ability to model the temporal aspects of episodic memory in non-human animals has been challenging and controversial. This article briefly reviews the theoretical perspective in which temporal processing plays a prominent role in episodic memory. Next, the article reviews experimental attempts to identify temporal processes of episodic memory in animals. Recent studies suggest that, at the time of memory assessment, rats remember a unique earlier event, including when it occurred, what happened, and where it took place, referred to as what-where-when memory.

Keywords

Episodic memory; Episodic-like memory; What-where-when memory; Animal models; Temporal information processing; Unexpected question; Binding; Interference

1. Introduction

1.1. Episodic memory in people

For over a decade, researchers have undertaken an extensive effort to identify processes in non-human animals (henceforth animals) that bear some relationship to the case of episodic memory in people. Episodic memory may be defined in at least two ways. Defined from the perspective of content, episodic memory stores representations of unique, personal past events. Defined from the perspective of experience, episodic memory has been described as re-experiencing a unique personal past event. People report both aspects of episodic memories, and failures of memory may occur in either domain.

Episodic memory is distinguished from semantic memory. Semantic memory stores representations of facts about the world, without information about the context in which the memories were stored. By contrast, episodic memory includes contextual information that occurred at the time of memory storage. Moreover, it has been argued that the subjective experiences that accompany retrieval, such as conscious recollection or the experience of the event re-occurring, are critical aspects of episodic memory [58,59,61,62]. Studies of human memory can exploit both behavioral and subjective sources of information, and both sources have provided rich opportunities for generating hypotheses about human memory. However,

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the development of animal models of human memory focuses exclusively on behavioral sources of evidence because subjective sources cannot be evaluated in non-verbal animals. Therefore, Clayton and colleagues [8] developed behavioral criteria for studying episodic memory that focus on Tulving's [60] classic definition of episodic memory: *what* happened, *where* did it occur, and *when* did it take place. Thus, *what-where-when* memory focuses on the content of episodic memory, which can be evaluated in animals. Because behavioral criteria do not assess subjective experiences, Clayton and Dickinson [9] introduced the term *episodic-like* memory to describe the content of episodic memories in animals.

1.1.1. Unique episodes—A critical aspect of episodic memory is that they are memories for *unique events or episodes*. Therefore, a primary goal of research that seeks to evaluate evidence for episodic-like memory in animals is documentation that the memory is about a specific earlier event. Critically, it is necessary to rule out alternative explanations that may exploit rules or strategies that do not require memory for a unique event. Although there are many efforts underway to examine elements of episodic memory in animals, as exemplified by the articles in this *Special Issue*, it is fair to state that all of these approaches share the common need to rule out alternative explanations that may use simple rule-based algorithms to solve behavioral tasks, if these tasks are to be judged as valid models of episodic memory.

1.1.2. Mental time travel—The mental-time-travel hypothesis may be regarded as at the interface between behavioral and subjective processes in episodic memory. According to the mental-time-travel hypothesis, episodic-memory retrieval involves travelling back in time to re-experience an earlier episode. Mental time travel has traditionally been described in subjective terms that focus on autonoetic consciousness, that is the ability to re-experience oneself in the remembered event, which is linked to self awareness [58,61,62]. However, Roberts and colleagues [45,47,48] have recently described mental time travel in behavioral terms. With respect to episodic memory, Roberts and Feeney [47] proposed a cone-shaped structure to represent episodic memories as a function of time into the past. Mental episodes have the greatest clarity and sensory detail when they are relatively close to the current time, and these dimensions decline as the mental event recedes farther into the past. The length of the cone represents time into the past, and the width of the cone represents the amount of detail about the remembered events at different points in time. It is worth noting that a critical aspect of Roberts and Feeney's proposal is the ability to represent a specific point in time, which will be discussed in greater detail in the next section.

2. The role of temporal processing in episodic memory

It has long been proposed that animals do not have episodic memories [59,60] and do not engage in mental time travel [44,56]. Experimental attempts to demonstrate episodic-like memory (discussed below) and planning for the future (another aspect of mental time travel but beyond the scope of this article) have been met with caution and considerable debate [54,55]. Part of the difficulty in making progress on this problem has been a lack of agreement about standards by which to judge proposed cases of episodic memory in animals. There are clear examples of alternatives to episodic memory, for example judgments of relative familiarity (discussed in greater detail below). But what exactly are episodic memories? Mental time travel is only of limited help in answering this question because mental time travel may be regarded as a metaphor rather than as a psychological process. In this respect, Roberts and colleagues [47,48] have provided some theoretical clarity. Roberts and colleagues [48] proposed that episodic memories include a representation of the *time of day* at which an earlier event occurred. This definition of *when* is to be distinguished from alternative ways to judge the temporal distance of an event which do not include a representation of the event; for review, see [31].

Two events that occurred at different times in the past can be dated in multiple ways, and not all methods correspond to episodic memory in people. One way to date an event is to remember the *time of occurrence* of the event within a temporal dimension [32]. People do this in multiple ways, for example by remembering that an event occurred in the morning, on Tuesday, in 2001, in the summer, etc. Importantly, according to this proposal, a specific event is remembered, including the time at which it occurred. This proposal is consistent with Clayton and colleagues' definition of what-where-when memory. Gallistel proposed that a network of oscillators with multiple periods may be used to represent the time of occurrence of events, and recent research on time perception supports the hypothesis that animals have the basic building blocks to represent time of occurrence (i.e., multiple oscillators across a broad range of periods) [17,19–21,25,26]; for review see [22,23].

Although an event may be dated by remembering the time of occurrence of the event, there are alternative ways that the relative age of an event may be judged. One major category by which the age of an event may be judged is by timing an elapsing interval with respect to the occurrence of the event [7]. According to this proposal, the amount of time elapsed since the occurrence of the event is monitored on a moment to moment basis, but, critically, this can be done *without* remembering specific aspects of the initiating event. Therefore, an elapsing interval is a non-episodic-memory solution that may provide temporal information without remembering the specific episode. More broadly, the relative ages of two events may be discriminated by judging the *relative familiarity* of these events (presumably the more recent event is more familiar than an earlier event). Again, critically, this is a non-episodic-memory solution that provides temporal information without remembering a specific episode.

The *when* component of what-where-when memory has been the most difficult to document. The difficulty stems from both a history of unsuccessful attempts to document it and from challenging conceptual issues. With respect to unsuccessful attempts, it is worth noting that these studies [e.g., 6,34,49] were successful in documenting *what* and *where* memory but did not document *when* memory. Thus, it may be the case that the temporal component of what-where-when memory is fragile, unstable, difficult to train, or some combination of the above challenges. Thus, some methods may be sufficient to document what-where-when memory, while other methods may not be sufficient. At the conceptual level, it is difficult to establish that an animal *remembers* something rather than merely *knowing* it [35]. This conceptual problem is compounded because introspective data are not available in animal research. The focus of the research reviewed below emphasizes the need to pinpoint the content of memory in episodic memory as a representation of a unique earlier event, while ruling out alternative, non-episodic strategies.

3. Experimental attempts to identify temporal processes of episodic memory in animals

3.1. What-where-when memory

A number of experiments have tested the hypothesis that animals remember what, where, and when about a specific event. These experiments focused on Tulving's [60] classic definition of episodic memory and Clayton's behavioral criteria for episodic-like memory [8]. This section will review initial experiments that established evidence for what-where-when memory in scrub jays and rats. Next, a series of experiments that sought to identify the temporal processing involved in what-where-when memory will be reviewed.

3.1.1. Episodic-like memory in scrub jays—Clayton and Dickinson's [9] classic experiment provided the first evidence of what-where-when memory in non-humans. Their approach was to provide food-storing scrub jays with opportunities to cache and retrieve two

food types that differed in terms of palatability and perishability. Jays prefer wax worms over peanuts, but peanuts are harder than wax worms, which decay over time in nature. Clayton and Dickinson hypothesized that the scrub jays would readily learn about the experimental contingencies that governed the availability and freshness of the foods that the birds had cached earlier. In their experiment, the scrub jays cached either peanuts followed by wax worms, or on other occasions, worms followed by peanuts. The birds were permitted to retrieve the caches after a short or long retention interval. For some scrub jays, the worms decayed after a long retention interval, and for other birds they were replenished with fresh worms. Peanuts did not decay, and worms were always fresh after a short retention interval. The scrub jays quickly learned to prefer the worm rather than the peanut cache sites when the worms were fresh, but this preference was reversed when the worms were decayed. Critically, these data suggest that the scrub jays are sensitive to *what* (food type), *where* (location in a tray), and *when* (time of caching and recovery). In follow up studies, Clayton and colleagues [10–14,28] have demonstrated that scrub jays have a detailed representation of what, where, and when food was cached. Recently, two other food-storing birds, magpies [69] and black-capped chickadees [29], have been shown to have what-where-when memories of food caches.

3.1.2. Episodic-like memory in rats—We adopted Clayton's approach to ask if rats have what-where-when memories. Our experiments [1–3,68] showed that rats have a detailed representation of what, where, and when specific events occurred. In this section, initial evidence for what-where-when memory is described. In the next section, studies that identify the temporal processes that subserve what-where-when memory are described.

The rats were trained in an eight-arm radial maze, which has eight runways radiating from a central hub. In a standard radial maze experiment, a small piece of food (i.e., consumed in its entirety upon discovery) is obtainable at the distal end of each location. The rat is permitted to explore the maze and consume all of the food. Because the food is consumed in its entirety when discovered and no additional food is available after consumption in a standard radial maze experiment, the optimal strategy for a subject is to visit each location once and only once. Extensive evidence indicates that rats perform at a near-optimal level and that they do so based on memory for recently visited locations [40,46].

Babb and Crystal [3] used a modified version of the standard radial maze experiment as follows. The trial was divided into three parts: a *study* phase, a retention interval, and a *test* phase. The retention interval interrupted the trial, which otherwise continued from study to test phases. We use the terms *study* and *test* because the locations of food in the test phase depended on memory for locations of food in the study phase. In the study phase, four locations were randomly selected to provide food (the other arms were blocked by closed guillotine doors). Two of the study locations had standard chow-flavored food. One of the study locations, randomly selected each trial, had a distinctive grape-flavored food, and one study location, also randomly selected, had a distinctive raspberry-flavored food. After eating its first helpings of food in the study phase, the rat was removed from the maze for a retention interval which was either short (1 hr) or long (6 hr). The rat ate its second helpings of food in the test phase, at which point the trial was a continuation of the study phase. All doors were open in the test phase, but food was never available at the chow locations that had been visited in the study phase. By contrast, the locations that were closed in the study phase provided chow-flavored food in the test phase. Thus the test phase is a test of memory for recently presented information from the study phase (i.e., memory about the study phase was required to avoid visiting now-depleted chow locations). The locations that recently had grape and raspberry replenished grape and raspberry, respectively, after a long retention interval, but not after a short retention.

Optimal performance in the task described above required what-where-when memory. The rats received replenishment of distinctive flavors after one, but not the other, retention interval. Consequently, a temporal component was required to efficiently revisit the locations that were about to replenish, and reduce this tendency at other times. The rats showed evidence of what-where-when memory. They revisited the grape and raspberry locations at a higher rate when these locations were about to replenish relative to occasions when these locations were not about to replenish. This could only be accomplished if they remembered the locations that recently had a distinctive flavor and temporal information about the study and test phases. The rats accomplished this differential rate of revisiting grape and raspberry locations while maintaining high accuracy in avoiding revisits to chow locations (which never replenished).

Next, we tested the hypothesis that rats have content-selectivity of what-where-when memory. Our objective was to determine if the rats remembered the *specific* flavors (grape vs. raspberry) that were encountered in the experiment described above. To accomplish this objective, we devalued one of the distinctive flavors, while leaving the other intact. In one experiment, we satiated the rats to one of the flavors (grape or raspberry) during the long retention interval while leaving the other flavor intact; we used a flavor-specific devaluation [4,15]. When the trial continued after access to one of the flavors, the rats selectively reduced revisits to the devalued flavor while continuing to revisit the location with the non-devalued flavor. In another experiment (with banana and chocolate distinctive flavors, using the same rats), during the long retention interval, we devalued chocolate by pairing it with lithium chloride; we used a learned taste aversion manipulation [5,38]. The rats selectively eliminated revisits to the chocolate location without reducing revisits to the banana location. These data suggest that the rats remember the specific flavors that were encountered at the locations, in addition to temporal information.

3.2. Temporal processing in what-where-when memory

In the experiments described above, the rats adjusted revisit rates after different retention intervals at the appropriate locations, which suggests the use of what-where-when memory. But what type of temporal mechanism was used? And is memory of a *specific episode* required to accomplish the adjustment in revisit rates (i.e., is it *episodic* memory)? There are three types of temporal information that were available to support what-where-when memory. First, because the trials always started at an approximately constant time of day, the test phases also occurred at approximately constant times of day (i.e., 1 or 6 hr later). Therefore, time of day at the *test* phase could be used as a cue to adjust revisit rates. Second, the *interval* between study and test phases could be used to adjust revisit rates to the distinctively baited locations. Third, the rats might have remembered the specific study episode, including *when* (i.e., the time of day at which) the *study* event occurred. Importantly, the third proposal, but not the first two proposals, requires memory of the study episode. Thus, discrimination of time of day at test or timing an interval with respect to an earlier event represent alternative explanations of what-where-when memory that would not require episodic memory.

A number of experiments have investigated the temporal information that rats used for the *when* component of what-where-when memory. Three investigations will be reviewed.

First, Babb Crystal [1] tested the hypothesis that rats were using time of day at the test phase as a cue to solve the discrimination of what, where, and when. To test this hypothesis, we held constant the time of test after both short and long retention intervals. We did this by using 1 and 25 hr retention intervals, and starting the study phases at an approximately constant time of day. Chocolate replenished at its trial-unique location after a 25-hr retention interval, but not after a 1-hr retention interval. For example, consider a rat that has its study

phase start at 1200. The test phase began 1 or 25 hr later. If the retention interval was 1 hr, then the test phase began at 1300 on the *same day* as the study phase. By contrast, if the retention interval was 25 hr, then the test phase began at 1300 on the *next day*. Note that it was 1300 at test after either short or long retention intervals. Thus, time of day at test could not be used to adjust revisit rates at the chocolate location. Yet the rats revisited the distinctively baited location at a higher rate when it was about to replenish relative to times when it was not about to replenish. The differential revisit rate clearly could not be based on time of day at test because it was the same time of day in both retention interval conditions. Note that the time of study was also constant (1200 in the example above). Thus, a potential solution to the task is to estimate the time since the study phase. This could be accomplished by timing an interval between study and test. Alternatively, the rat could encode the time of occurrence of the study phase and current time of occurrence and obtain the interval by subtraction [32]. Using an independent method, we showed that rats can discriminate alternate days [42]. Because 1- and 25-hr retention intervals produced tests that occurred at the same time of day on alternate days, the discrimination of alternate days (e.g., noon today vs. noon yesterday) is another mechanism by which the animals may have solved this what-where-when task. Recently, Naqshbandi and colleagues [39] replicated our study using somewhat different methods, which provides additional evidence that rats have what-where-when memories and that rats did not solve the discrimination by using time of day at the test phase.

In a second investigation on temporal information in what-where-when memory, Roberts et al [48] carefully selected the times at which study and test phases occurred to eliminate the correlation between time of study and interval between study and test. In the Roberts et al. study, some trials had study phases that started at a constant time of day (thereby having test phases at varying times of day); other trials had the test phases occur at a constant time of day (thereby having study phases start at varying times of day). The time of day at which study and test phases occurred and the retention interval between study and test were arranged so that some rats received a *consistent replenishment pattern* with respect to time of study (referred to as the *when* group), retention interval (referred to as the *how-long-ago* group), or both (the *when + how-long-ago* group). The *when* group failed to learn the replenishment contingency whereas the other two groups adjusted revisit rates to correspond with the replenishment contingency. It should be noted that rats in the *when* group received *inconsistent* feedback (i.e., replenishment) after short and long retention intervals. A potential explanation of these data is the hypothesis that when both *when* and *how-long-ago* information are available, rats appear to rely on *how-long-ago* (or learn about it more rapidly); this may be a form of overshadowing, which occurs under conditions of cue competition [27]. This hypothesis does not preclude the possibility that time of study may be encoded, but different experimental techniques might be necessary to reveal remembering of when the study episode occurred.

In a third investigation on temporal-information processing in what-where-when memory, Zhou and Crystal [68] sought to evaluate what-where-when memories under conditions in which *how-long-ago* cues were irrelevant to predicting replenishment. Because the data of Roberts et al. [48] suggest that *how-long-ago* dominates when multiple temporal cues are available, we made *how-long-ago* cues *irrelevant* to predicting replenishment. When *how-long-ago* was rendered irrelevant, we found evidence for remembering *when* (i.e., time of day) an earlier study episode occurred, in addition to knowledge of *what* occurred and *where* it took place. In the Zhou and Crystal study, rats were tested in the morning or afternoon (but not both) on separate days (see Fig. 1a). Chocolate replenished at a daily unique location at only one of these times (morning for half of the rats; afternoon for the other rats). The interval between the study and test phases (which occurred on the same day) was constant (approximately 2 min). Because the location of chocolate varied across days and

the morning and afternoon sessions were presented in random order, what-where-when memory would be needed to seek out the chocolate location selectively on occasions when chocolate was about to replenish. When the chocolate location was about to replenish, the rats revisited that location at a higher rate relative to non-replenishment trials (Fig. 2a). These data suggest that rats used what-where-when memories to adjust revisit rates to the daily-unique chocolate location. Importantly, what-where-when in this study could not be based on the delay between study and test (i.e., it could not be based on judging relative familiarity of the study items or timing an interval between study and test).

Next Zhou and Crystal [68] sought to determine the type of timing mechanism used in what-where-when memory. There are two remaining hypotheses. According to the *circadian time-of-day* hypothesis, the rats used a circadian signal (i.e., morning vs. afternoon) [32,57] to adjust revisit rates at the daily-unique chocolate location. Alternatively, according to the *interval-timing* hypothesis, the rats timed the interval from light onset in the colony to the morning and afternoon sessions. Morning sessions occurred 1 hr after light onset in the colony, and afternoon sessions occurred 7 hr after light onset. Consequently, we used a phase shift of 6 hr to test these hypotheses. The lights in the colony were turned on 6 hr early and the probe session was conducted at the usual time in the morning (see Fig. 1b).

According to the circadian time-of-day hypothesis, the rats would treat the probe as a morning session because an endogenous circadian oscillator is not expected to adjust immediately to a phase shift [32,33,57]. Alternatively, according to the interval-timing hypothesis, the rats would treat the probe as an afternoon session because afternoon sessions typically occur 7 hr after light onset in the colony; there is independent evidence that rats can time short and long intervals with respect to colony-light onset in the range of hours [17]. The rats did not use the interval between light onset and the session, suggesting that they used circadian time of day (Fig. 2b). Next, we sought to determine if it was the *time of day* at *study* or at *test* that was responsible for the different rates of revisiting the chocolate location. Because a 2-min delay between study and test is too small for rats to discriminate based on a circadian oscillator [43], we increased the delay to 7 hr (see Fig. 2c). Importantly, the time of day at study was *familiar* from prior training, but the time of day at test was *unfamiliar* (approximately 7 hr later than usual). Consequently, if the rats used time of day at study, then they should continue to differentially revisit the chocolate locations. Alternatively, if the rats used time of day at test, then there is no basis for them to revisit chocolate locations at different rates in the morning and afternoon because the test times were unfamiliar. When tested with *novel* test times of day after *familiar* morning or afternoon study times of day, we observed complete transfer (i.e., the differential rates of revisiting occurred on the very first trial in the morning and the very first trial in the afternoon; Fig. 2c–d). These data suggest that at the time of memory assessment, the rats remembered the time of day at which the study episode occurred. We obtained additional evidence for the same conclusion by conducting a conflict test. Because the 7-hr delays between study and test phases produced a 1-hr overlap between the two types of trials, it was possible to start a trial with a late study phase and end the trial with an early test phase (see Fig. 1d). Again we sought to determine if the rats were adjusting revisit rates in the test phase based on the time of day at test (we refer to this proposal as the *test-time* hypothesis) or based on *memory* of the time of day at which the study phase occurred (referred to as the *study-time* hypothesis). According to the test-time hypothesis, the rats should revisit at the usual baseline rate that typically occurred on tests at that time of day. Alternatively, according to the study-time hypothesis, the rats should revisit at the usual time of day that occurred after a later study time (which usually is followed by a test 7 hr later rather than 1 hr later). The rats adjusted chocolate revisits based on the time of day at study rather than the time of day at test (Fig. 2e). These data also suggest that rats remembered the study episode, and the time of day at which the study episode occurred.

At the time of memory assessment, the rats remembered the time of day at which the study episode occurred. Importantly, these experiments suggest that rats remember what-where-when under conditions in which how-long-ago cues were made irrelevant to performance. Thus, the *relative strength* of memories that decay over time (i.e., *relative familiarity* of study items) *cannot* explain our results because the delay between study and test phases was constant in each experiment.

We argued that rats, at the time of memory assessment, remember when the study episode occurred, in addition to what happened and where it took place based on a single, brief encoding episode [68]. Recent evidence suggests that male meadow voles anticipate the sexual receptivity of female voles based on a brief encoding episode that includes time of day, the stage of postpartum estrus, and location of the encounter [30]. Honey bees also integrate time of day with visual and place information based on a single brief encoding episode [41,67]. The ability to use what, where, and when based on time of day may be quite widespread.

Experiments with rats have examined retention intervals as long as 25 hr. By contrast, scrub jays have shown what-where-when memory after 5 days [e.g., 9]. It is not known whether rats could remember over such a long retention interval, although techniques to promote long-lasting memories are available [24] and may be expanded. An interesting question for future research is to increase the retention interval and explore the temporal mechanisms that might support memory in these cases. Time of day within a single day may be based on the phase representation of a circadian system. However, to distinguish time of day across multiple days, additional timing mechanisms would be needed. For example, we recently showed that rats can discriminate alternate days [42]. Gallistel [32] has proposed that multiple oscillators, each with unique periods, may be used to represent the time of occurrence of events in a calendar-date system. Extending the dissociation of how-long-ago and time of day beyond a single day represents a significant challenge for future research.

4. Other approaches: Converging lines of evidence

The goal of the research reviewed above is to test the hypothesis that rats have episodic-like memory (i.e., they remember a specific episode including specific details of what, where, and when the event occurred). The validation of an animal model of human memory holds great potential for gaining insight into the neurobiology of human memory and disorders of memory. However, this effort is likely to require convergent lines of evidence [18,51]. It may be argued that any single approach is likely to be limited by a set of competing, alternative explanations. Thus, a careful selection of multiple approaches may overcome weaknesses that may exist if each approach were treated separately. The variety of approaches that researchers have taken to tackle the difficult problem of investigating episodic memory in animals is exemplified by the other articles in this Special Issue. This section will briefly review three other approaches that may promote progress in the development of convergent lines of evidence for episodic-like memory in rats.

4.1. Unexpected question

A fundamental aspect of episodic memory is that it can be used to report information when the test of memory is unexpected. One problem with many of the paradigms used to evaluate episodic-like memory is that extensive training is required [52,64–66]. Zentall and colleagues have argued that it is not possible to preclude semantic-like knowledge in the discrimination of what-where-when because the contingencies of food availability are explicitly trained; the explicit training might foster the development of semantic knowledge about experimental contingencies. Therefore, they proposed that it is preferable to assess the capacity for episodic-like memory in animals by using an unexpected question about a

recent event. Accordingly, they proposed that documenting episodic-like memory requires a demonstration that the animal can report on a recent event when there was no expectation that such a report would be required (i.e., answer an unexpected question).

Zentall and colleagues [66] trained pigeons in a symbolic matching-to-sample task that may be thought of as responding to the nonverbal question “Did you just peck or did you just refrain from pecking?” The presentation of one line orientation signaled that a particular behavior (i.e., pecking or its absence) was required, which was then followed by the requirement to select one color to obtain reward. Next, the pigeons were provided with conditions that elicited pecking or the absence of pecking, but without the requirement (and hence without the expectation) that a report about the pecking behavior would occur. In the test, the sample stimuli that elicited pecking or the absence of pecking were presented, but these stimuli would not be expected to elicit the expectation of a forthcoming question about pecking. Next, the birds were unexpectedly provided with the opportunity to report about their recent behavior (pecking vs. not pecking). When the pigeons were first presented with the unexpected question, they reported accurately that they had or had not recently pecked. In a further test, the birds were presented with a novel event that elicited pecking (i.e., a new stimulus that occasioned generalized pecking) or a novel event that elicited the absence of pecking (i.e., presentation of no stimulus on the test). Next, when the birds were unexpectedly asked if they had recently pecked, they again accurately reported that they had or had not pecked.

Singer and Zentall [52] pointed out that the presence vs. absence of pecking may give rise to proprioceptive cues that may be present when the unexpected question occurs. Consequently, the discrimination of motor aftereffects is an alternative explanation to the use of episodic-like memory to answer the unexpected question. To circumvent this problem, Singer and Zentall trained pigeons to report on the *location* of a previous response, which should produce equivalent motor aftereffects (i.e., answering the nonverbal question “Where did you just peck?”). As a further precaution, after a left or right initial response, the birds were required to peck at a center stimulus, thereby reducing the likelihood that the position of the beak could serve as a cue at the time of test. Thus, the birds were trained to report which side they had pecked earlier (i.e., before pecking the center). Next, the pigeons were trained on a symbolic-matching task which produced a peck on the left or right side that was an *incidental* part of the task. In the test, the trial started with the symbolic-matching task but continued (for the first time) with the presentation of a center stimulus and an opportunity to report which side had incidentally been pecked at an earlier stage in the test. When the pigeons were first asked the unexpected question, they reported accurately whether they had pecked on the left or right side. These data suggest that pigeons can retrieve information about a past event, although the location of the matching stimulus had never previously been requested.

It should be noted that episodic memory is generally regarded as a kind of long-term memory. Therefore, it is noteworthy that the experiments on unexpected questions have thus far used relatively short delays between encoding and test (0–2 sec).

The evidence reviewed in the sections above suggests that, at the time of memory assessment, rats remember features of the study episode. It would be valuable to develop a converging line of evidence that rats can answer an unexpected question. Such a converging line of evidence could use operant methods, following Zentall’s approach, or it could be integrated into tests of what-where-when memory on the radial maze.

4.2. Binding

A critical element of episodic-like memory is that the retrieved memory is about a single event. Therefore, it has been argued that the representation of what-where-when should be integrated [8]. Skov-Rackette, Miller, and Shettleworth [53] developed tests designed to determine if what, where, and when information are represented as integrated or independent memories. Skov-Rackette and colleagues trained pigeons in a matching to sample task using one of two colored shapes, one of eight locations on a touch screen, and one of two retention intervals (2 vs. 6 s). Three types of test phases could occur after presentation of the sample and retention interval, contingencies corresponding to what, where, or when. After training with the three types of assessments, the birds accurately reported identity of the sample, its location, and the length of the retention interval.

To assess whether identity, location, and time were encoded independently or bound together in memory, Skov-Rackette and colleagues [53] presented two different tests in succession on occasional non-rewarded probes. They hypothesized that if any of the features were stored in independent memories, the probability of responding correctly on the second test should be independent of the probability of responding correctly on the first test of the same trial. By contrast, if all three elements (what, where, and when) are bound in an integrated representation of the preceding event, then it should be possible to document dependence between the two successive tests of accuracy. Performance on the second test was unrelated to performance on the first test, suggesting that although the birds remembered all aspects of the sample presentation, they may accomplish this based on independent memories for each of the features. However, there are technical challenges associated with documenting dependence even if what-where-when is integrated. Skov-Rackette et al. noted that the second test occurred rarely and that the presentation of a test previously signaled the end of the trial (which is a cue to forget the sample [50]). Consequently, an alternative approach would be to train the animals with multiple tests from the outset and evaluate independence in this case. Moreover, the second test may suffer from output interference that necessarily occurs when completing the first test [16,63].

The data from Skov-Rackette and colleagues (2006) suggest that although multiple features of an event (e.g., what, where, and when) may be encoded from the presentation of a single event, it is possible to do so without remembering a single, multi-dimensional event. This study highlights the importance of testing for an integrated representation of a single event.

Although pigeons did not appear to have an integrated representation of what, where, and when, Iordanova, Good, and Honey [37] documented integrated what-where-when memories in rats. In the Iordanova et al study, an auditory stimulus (what: X or Y) was presented in location (where: context A or B) and temporal (when: morning or afternoon) contexts. X occurred in context A and Y in context B in the morning, but in the afternoon, these arrangements were reversed (X in B and Y in A). Next, X (but not Y) was paired with footshock at midday. In a subsequent test of contextual fear to A and B in the morning and afternoon, rats showed more fear in A than in B in the morning and the reverse data pattern (more fear in B than in A) occurred in the afternoon. Thus, this study documents an integration of what (X or Y), where (A or B) and when (morning or afternoon). Evidence for integration of what, where, and when has also been documented with rhesus monkeys [36]. This study used a computerized task similar to [53] but found evidence for integration of what-where-when memory.

4.3. When: Combating interference from a previous trial

An important aspect of remembering a specific, unique event is the ability to distinguish it from competing memories of temporally similar events. A major impediment to

distinguishing between similar events is interference. The temporal spacing between events contributes significantly to the development of proactive interference, in which earlier events interfere or inhibit memory of a subsequent item; for review see [63]. For example, in *same/different* list learning tasks, a number of items (e.g., pictures or sounds) are presented in a list. A probe item is presented, and the subject is required to indicate if that item is *same* (presented in the list) or *different* (absent from the list). Use of items that repeat from time to time produces interference; the conundrum for the subject is that the probe item may be familiar because it was in the current list or because it was presented in an earlier list. One way to make the task more difficult is to increase the retention interval. One solution to this problem is for the subject to adjust a criterion level of familiarity so that very recently presented items (i.e., from the current list) are above the criterion, but items presented earlier (i.e., from other lists) fall below the criterion.

Wright [63] has noted that a *same/different* list learning task can be made more difficult by increasing item repetitions in the memory task. This would introduce a *same* bias because all items would be more familiar. Importantly, there is no adjustment that can be made to a familiarity criterion that will restore their accuracy levels. Wright proposed that, in this situation, the subject may change its memory strategy from a familiarity process to a more recollective memory process. Importantly, a recollective process would involve recollecting what items were presented in the current trial and what items were presented in past trials. Thus, it may be possible to show that a subject knows *when* the item was presented.

5. Conclusions

The focus of this review was on the need to document that a proposed model of episodic memory in animals is based on a representation of a unique past event. One way that an event is isolated in the past is that it occurred at a *specific* point in time. The term *time* has multiple meanings, and only some of these meanings require a representation of an earlier episode. A number of studies suggest that rats, at the time of memory assessment, remember when (i.e., the time of day at which) a specific event occurred in addition to its location. These types of experiments provide insight into the type of temporal representational system that rats may use in episodic-like memory, namely a representational system that maintains the time of occurrence of encoded episodes.

Acknowledgments

Supported by National Institute of Mental Health grant R01MH080052 to JDC.

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Fig. 1.

Experimental design of Zhou and Crystal's study [68]. **a.** Design of Experiment 1. The morning or afternoon was randomly selected for presentation of first helpings (study phase) and second helpings (test phase) of food. The figure shows an example of the accessible arms and flavors in a study phase and the corresponding test phase that would occur after a 2-min retention interval. Chocolate or chow flavored pellets were available at four randomly selected arms in the study phase; access to the other four arms was prevented by closed doors. After a 2-min delay, chow-flavored pellets were available at previously inaccessible locations in the test phase. In the replenishment condition, chocolate replenished at the location that had chocolate in the study phase (shown for the morning session); in the non-replenishment condition, chocolate did not replenish at the other time of day (shown in the afternoon session). Chocolate replenished at second helpings in the test in the morning (7 a.m.) session but not in the afternoon (1 p.m.) session for half of the rats; these contingencies were reversed (not shown) for the remaining rats. For each rat, one session (i.e., first and second helpings) was conducted per day. The same arms were used to illustrate morning and afternoon sessions in the figure to facilitate inspection of presence and absence of chow and chocolate, but these arms were randomly selected in each session for each rat. **b.** Phase-shift design of Experiment 2. Light onset occurred at 12 a.m. (i.e., 6 hr earlier than in Experiment 1) and the first and second helpings occurred at the time of a typical morning session (i.e., starting at 7 a.m.). Note that 7 hr elapsed between light onset and the study-test sequence (solid horizontal line), which is comparable to the time between the typical light onset and a typical afternoon session (dashed horizontal line) in Experiment 1. The design of the experiment puts predictions for time-of-day and how-long-ago cues in conflict. Thus, a rat would be expected to behave as in its morning baseline (based on time of day) or as in its afternoon baseline (based on how long ago). **c.** Transfer-test design of Experiment 3. The time of day at which first helpings occurred was the same as in Experiment 1 (i.e., 7 a.m. in early or 1 p.m. in late sessions). The introduction of 7-hr retention intervals in Experiment 3 produced test phases that occurred at novel times of day (2 p.m. in early and 8 p.m. in late sessions). Early and late sessions had study times (but not

test times) that corresponded to those in Experiment 1. The first two sessions in Experiment 3 consisted of one replenishment and one non-replenishment condition. On subsequent days, an early or late session was randomly selected. Differential revisits to the chocolate location is expected if the rats were adjusting revisit rates based on the time of day at which the study episode occurred; revisit rates are expected to be equal in early and late sessions if the rats used time of day at which the test phase occurred. Study and test phases were as in Experiment 1, except that they were separated by 7-hr delays (shown by horizontal brackets). **d.** Conflict-test design of Experiment 4. The study and test phases occurred at 1 p.m. and 2 p.m., respectively. These times correspond to the typical time of day at which a late-session first helpings and early-session second helpings occurred in Experiment 3. The design of the experiment put predictions for time of day at study and time of day at test in conflict. Thus, a rat would be expected to behave as in its early-session, second-helpings baseline (based on test time of day) or as in its late-session, second-helpings baseline (based on study time of day). Reproduced with permission from Zhou W, Crystal JD. Evidence for remembering when events occurred in a rodent model of episodic memory. *Proceedings of the National Academy of Sciences USA*, 2009;106: 9525–9529. © PNAS.

Fig. 2.

a. Rats preferentially revisit the chocolate location when it is about to replenish in Experiment 1. The probability of a revisit to the chocolate location in the first four choices of a test phase is shown for replenishment and non-replenishment conditions; replenish and non-replenish sessions were presented in random order. **b.** Rats used time of day, rather than an interval, to adjust revisit rates in Experiment 2. Rats treated the study-test sequence as a morning session, suggesting the use of time of day rather than an interval-timing mechanism. The figure plots the difference between observed and baseline revisit rates. For the bar labeled interval, the baseline was the probability of revisiting chocolate in the afternoon; thus, the significant elevation above baseline shown in the figure suggests that the rats did not use an interval mechanism. For the bar labeled time of day, the baseline was the probability of revisiting chocolate in the morning; thus, the absence of a significant elevation above baseline is consistent with the use of time of day. The horizontal line corresponds to the baseline revisit rate to the chocolate location from Experiment 1. Positive difference scores correspond to evidence against the hypothesis indicated on the horizontal axis. **c.** and **d.** Rats preferentially revisited the chocolate location when it was about to replenish when the study, but not the test, time of day was familiar in Experiment 3. The probability of a revisit to the chocolate location in the first four choices of a test phase is shown for first replenishment and first non-replenishment conditions (**c**; initial) and for subsequent sessions (**d**; terminal). **e.** Rats remembered the time of day at which the study episode (i.e., first helpings) occurred in Experiment 4. Rats treated the novel study-test sequence as a late-session test phase, suggesting memory of the time of day at study rather than discriminating time of day at test. The figure plots the difference between observed and baseline revisit rates. For the bar labeled test time, the baseline was the probability of revisiting chocolate in the second helpings of the early session (test phase) in Experiment 3; thus, the significant elevation above baseline suggests that the rats did not use the time of day at test to adjust revisit rates. For the bar labeled study time, the baseline was the probability of revisiting chocolate in the second helpings of the late session (test phase) in Experiment 3; thus, the absence of a significant elevation above baseline is consistent with memory of the time of day at study. The horizontal line corresponds to the baseline revisit rate to the chocolate location from Experiment 3 (terminal). Positive difference scores correspond to evidence against the hypothesis indicated on the horizontal axis. **a–e.** Error bars indicate SEM. **a, c, and d.** The probability expected by chance is 0.41. Repl = replenishment condition. Non-repl = non-replenishment condition. **a.** * $P < 0.001$ difference between conditions. **b.** * $P < 0.04$ different from baseline. **c and d.** * $P < 0.04$ and ** $P < 0.0001$ difference between conditions. **e.** * $P < 0.001$ different from baseline. Reproduced with permission from Zhou W, Crystal JD. Evidence for remembering when events occurred in a rodent model of episodic memory. *Proceedings of the National Academy of Sciences USA*, 2009;106: 9525–9529. © PNAS.