

Episodic Memory in Nonhuman Animals Minireview

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Episodic memories differ from other types of memory because they represent aspects of the past not present in other memories, such as the time, place, or social context in which the memories were formed. Focus on phenomenal experience in human memory, such as the sense of ‘having been there’, has resulted in conceptualizations of episodic memory that are difficult or impossible to apply to nonhuman species. It is therefore a significant challenge for investigators to agree on objective behavioral criteria that can be applied in nonhuman animals and still capture features of memory thought to be critical in humans. Some investigators have attempted to use neurobiological parallels to bridge this gap; however, defining memory types on the basis of the brain structures involved rather than on identified cognitive mechanisms risks missing crucial functional aspects of episodic memory, which are ultimately behavioral. The most productive way forward is likely a combination of neurobiology and sophisticated cognitive testing that identifies the mental representations present in episodic memory. Investigators that have refined their approach from asking the naïve question “do nonhuman animals have episodic memory” to instead asking “what aspects of episodic memory are shared by humans and nonhumans” are making progress.

Introduction

Memory is not a single thing: our apparently seamless experiences of remembering result from the combined action of cognitively and neurobiologically distinguishable systems in the brain. These distinct systems have evolved because they each serve specialized functions that have promoted survival and reproduction [1]. One type of memory is episodic memory, which enables use of contextual information about distinct episodes from one’s personal past to guide behavior. For example, you might remember loading ripe tomatoes and watermelon for a barbecue on the supermarket checkout belt while reading about the anti-cancer properties of a plant in a tabloid headline. In this case, contextual information about where and when you formed a memory is useful in discriminating facts learned reading tabloids from facts learned during a trip to the botanical gardens. By contrast, semantic memories lack contextual details: you may know that monkeys have tails, but probably do not remember the occasion on which you learned this fact. The distinction between episodic and semantic memory in humans is central in cognitive neuroscience and has been well-established by the combination of behavioral studies, neuroimaging studies, and studies of patients with brain damage [2]. The extent to which these specific memory systems exist in nonhumans is debated. Some cognitive scientists argue that episodic memory may be uniquely human, at least in part because episodic

memory is often defined using criteria based in human conscious experience that are difficult or impossible to apply in nonhumans [3,4].

Comparative psychologists and neurobiologists who study the evolutionary and mechanistic relations among memory systems across species generally define episodic memory in terms that can be operationalized in objective studies with nonverbal species. Studies of memory in nonhuman animals have resulted in a rich set of methodologies, findings and perspectives. Mapping specific performances in nonhumans to human episodic memory remains controversial, but there is no doubt that our understanding of memory in humans and nonhumans is advancing. Here, we shall highlight some of the problems inherent in studying episodic memory in nonhumans and use selected examples to illustrate distinct perspectives and demonstrate progress. Central to our review is acceptance of the idea that episodic memories have distinct functional properties not found in other memory systems. It is possible to dissociate episodic memories from other types of memory based on the particular features of events that are mentally represented and the neurobiological systems that instantiate these representations [5,6]. These dissociations become possible when we design experiments based on the question, “what can an animal with episodic memory do that one without it cannot do?”

Moving beyond Anthropocentrism and Phenomenology

The term ‘episodic memory’ was coined by Endel Tulving in 1972 to describe a type of human memory, and was elaborated to apply to memory of autobiographical events resulting from ‘mental time travel’ associated with self-awareness or ‘autonoesis’ [3]. The first efforts to search for episodic memory in nonhuman species were therefore necessarily anthropocentric and faced the potentially insurmountable problem of mapping the objective performance of nonhuman animals in memory tests to human reports of the phenomenology of remembering. Debate continues about whether nonhuman animals ‘mentally travel in time’ and experience autonoesis [4,7], and these debates can shift attention away from the well-designed objective studies of nonhuman memory that yield progress (Figure 1). However, to the extent that these and similar phenomenology-rich conceptualizations of memory can be objectively operationalized, they will stimulate progress by challenging experimentalists to design better studies.

Natural selection has resulted in different memory systems because of the distinct functional roles these systems play in the service of overt behavior, not because of differences in the way these memories are phenomenally experienced. Nonetheless, some students of nonhuman memory continue to struggle with definitions of memory systems that emphasize phenomenology and private experience, arguing that “the main ingredient missing [in studies of episodic memory in nonhumans] is auto-noetic consciousness” [4]. This problem was famously sidestepped with the term ‘episodic-like’ to describe some memory in nonhumans [8]. Whatever terminology is used, progress will be most rapid when we define memory systems in entirely functional terms that can be objectively operationalized in behavioral experiments with a variety of species. As Bertrand Russell is believed to

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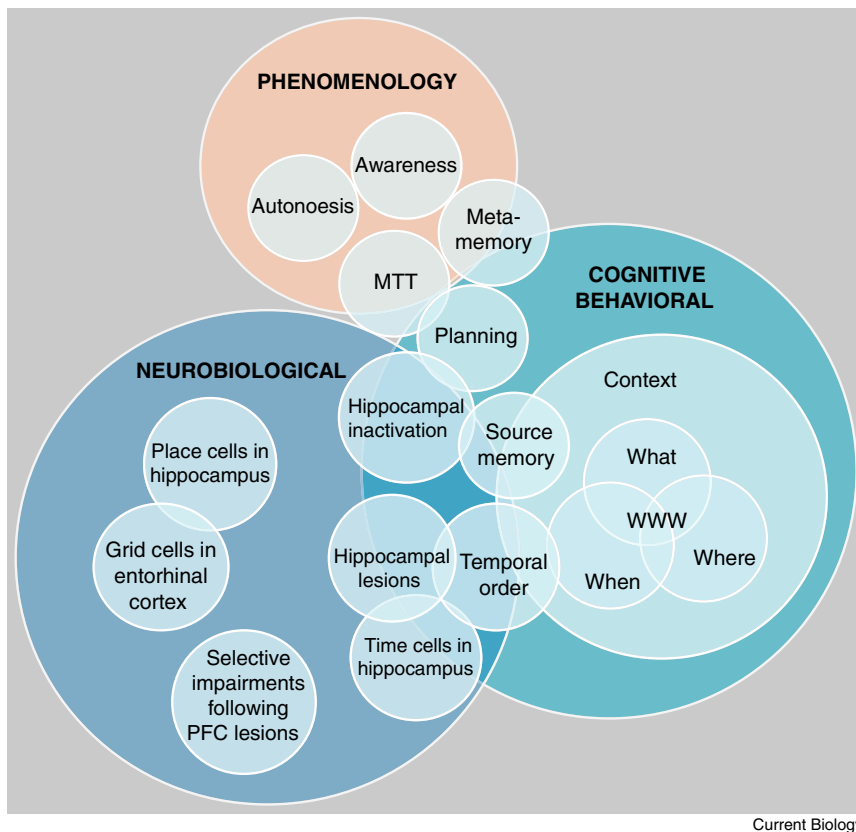


Figure 1. Constellation of mnemonic features of episodic memory.

Mnemonic features are grouped within the phenomenological, neurobiological, and cognitive behavioral approaches. Some areas of potential overlap are indicated. These are meant to be representative examples; there exist more mnemonic features, and more approaches, than could be depicted here. Future research might be directed at creating more overlap in the research domains indicated by the bubbles.

across species is a powerful method for establishing correspondences in memory systems. Whereas removal and inactivation of brain systems provide strong causal evidence regarding the locations of brain functions, electrophysiological recordings provide information about how processing in specific areas might be carried out. The representation of the spatio-temporal structure of sequences of events in hippocampal neural ensembles may be conserved across species (for review see [15]). During an odor-order test based on the one described above, the magnitude of changes in patterns of rat hippocampal ensembles predicted memory performance [16].

have stated: “The greatest challenge to any thinker is stating the problem in a way that will allow a solution.”

Neurobiological Approaches

Neurobiological manipulations can establish correspondences between specific memory capacities and specific neurobiological systems. Episodic memories in humans are particularly dependent on the integrity of the hippocampus and related structures, while other kinds of memory are not [9]. Because human episodic memory is known to be dependent on the hippocampus, determining which nonhuman memories are dependent on the hippocampus is one approach taken to episodic memory in nonhumans. After encountering a list of five odors in sequence, rats with hippocampal lesions were unable to report which odor occurred earlier in the list. By contrast, these rats could still correctly recognize whether an odor was familiar from having been presented during study and could discriminate one odor from another [10]. This dissociation of memory for order from the ability to recognize items parallels findings from humans, where hippocampal-dependent episodic memory is dissociated from other types of memory [11]. Similarly, monkeys with fornix transections, which disrupt one of two major afferent-efferent pathways of the hippocampus, were unable to make accurate recency judgments [12]. Subsequent lesion studies [13] and pharmacological inactivation studies suggest that, in the hippocampus, area CA3 and the dentate gyrus (DG) rapidly encode spatial separation, whereas area CA1 encodes temporal order (for example [14]).

Determining the extent to which similar kinds of neural processing, representing similar aspects of memory, occur

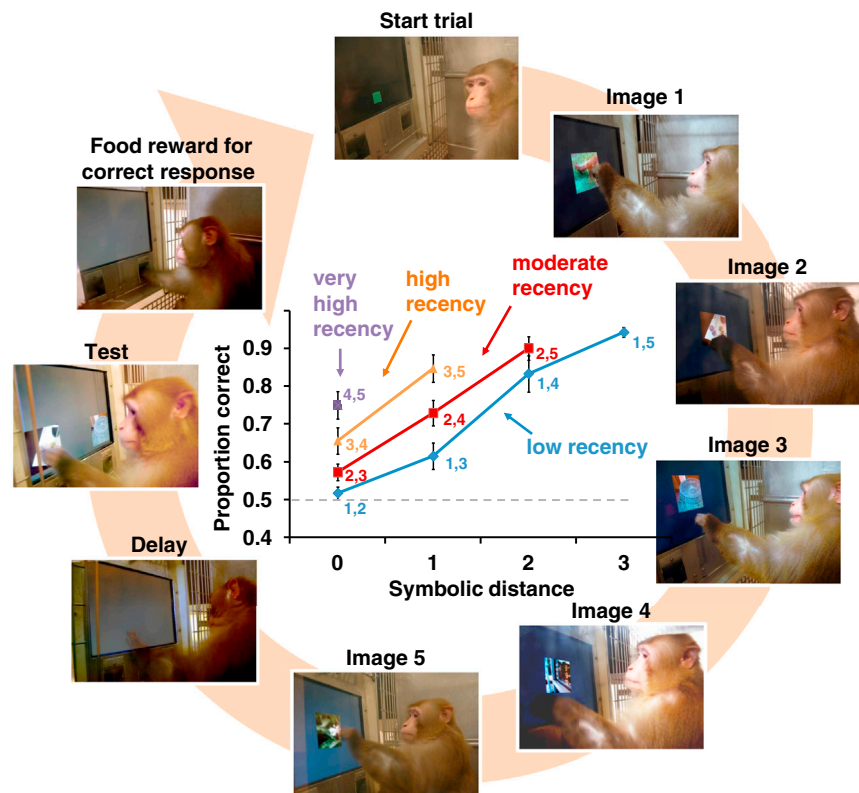
Specific ensembles have been shown to encode specific memories and likely the passage of time [17]. The lateral prefrontal cortex (PFC) in monkeys [18] and medial PFC in rats [19] also encode temporal order. Neural ensembles in the hippocampus have been found to ‘replay’ events encountered during spatial navigation tasks, with place cells firing in the same order during rest and sleep as they had when rats traveled a particular route. Similarly, the same neurons in the human hippocampus fire when subjects watch movie scenes and later recall them [20]. Disruption of this neural replay in rats impaired performance in a delayed alternation test, suggesting that reactivation of neural ensembles underlies memory for places recently visited [21]. Evidence that hippocampal cells in rodents encode time is accumulating [13,22], but it is still a challenge to establish direct parallels with humans, from whom relevant electrophysiological data are rarely collected. Less direct parallels are seen in human functional magnetic resonance imaging (fMRI) studies in which tests of temporal order result in activation of the hippocampus [23]. To the extent that discriminating the temporal order and locations in which events occurred are functional properties of episodic memory, these studies provide strong evidence for a homologous episodic memory function of the hippocampus among humans, monkeys, and rodents.

Cognitive Behavioral Approaches

Neurobiological studies of memory focus on identifying the brain areas and neural processes responsible for memory. Cognitive studies complement this work by establishing in more detail which aspects of events are represented, or stored, in the brain and how this information controls

Figure 2. Temporal order memory test for monkeys.

The images around the perimeter depict the stages in this behavioral test; the graph in the middle depicts typical results from averaging thousands of test trials. Trials began when the monkey touched the green square. The monkey then touched five trial-unique images presented one after the other. After a short delay, the monkey chose between a randomly selected pair of images from the list (here images 2 and 3; a '2, 3' test). Selecting the image that had appeared earlier in the study list was rewarded with a positive sound and a food pellet in the reward trough. The graph in center shows accuracy in tests with pairs of images from each combination of study list positions. Accuracy was higher for tests consisting of pairs that were widely separated in the study list (symbolic distance) and for images that were near the end of the list (recency). The dashed line indicates the accuracy expected if the monkey were guessing. Monkeys remembered the order in which images appeared, demonstrating an important property of episodic memory. (Adapted with permission from [30]).



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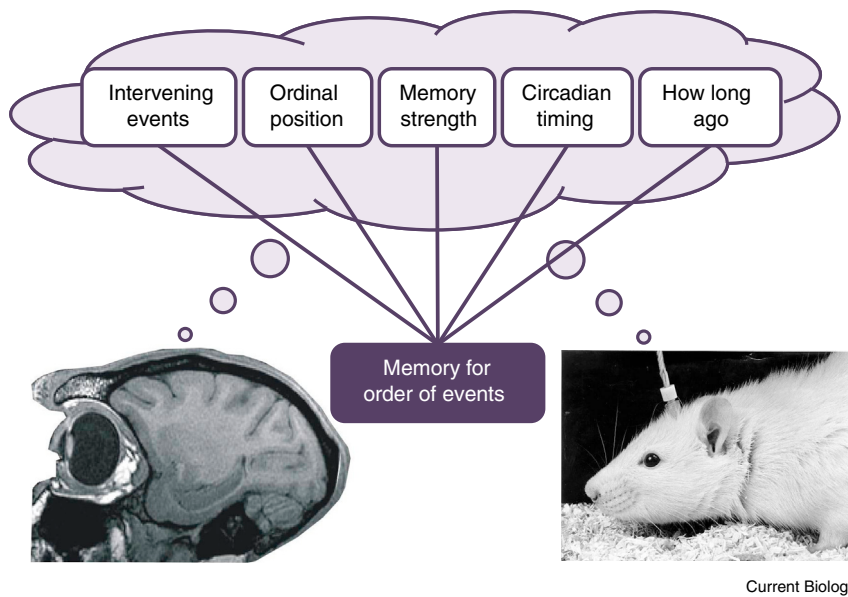
behavior (Figure 1). Episodic memory was described as memory for what happened, where and when (WWW memory) in food-caching scrub-jays (*Aphelocoma coerulescens*), birds that remember what foods they hid in which locations at which points in time [8]. Comparative researchers have developed analogous paradigms in other food-hoarding species (for example [24]), in rodents [25], and in primates [26]. Other behavioral paradigms for modeling aspects of episodic memory in nonverbal species include memory for temporal order [10], memory for the source of memories [27], and planning [7,28].

The many tests of whether particular species 'show' WWW memory equate to asking, "does species X have episodic memory?" This approach can be problematic for several reasons. Humans have many semantic memories that include what happened, where it happened and when it happened, such as knowledge of historical facts. We also have many episodic memories that do not include all three elements [29]. Surprisingly, when tests similar to the WWW tests designed to model episodic memory in nonhumans are conducted with humans, performance may not always depend on episodic memory [6]. A more nuanced approach tests the extent to which various species manifest different aspects of episodic memory, and has many advantages. First, we should expect memory to have evolved differently in different species so as to match their cognitive capacities to species-specific ecological demands, making a single conception of episodic memory overly restrictive. Focus on a single specific set of criteria can make it difficult to identify interesting and informative species-specific specializations in memory. Second, rather than simply rejecting behavioral paradigms as 'failures' to demonstrate fully-developed episodic memory if they do not meet a narrow definition, studying different aspects of episodic memory across species promotes new interesting areas of research to flourish.

Third, considering episodic memory as a constellation of mnemonic functions, rather than a single entity, may allow us to make best use of studies of nonhumans to illuminate the organization of memory more generally by identifying commonalities and differences among memory systems and across species. Studies of episodic memory in nonhumans may allow reevaluation of the type of memory we call episodic in humans and may better establish commonalities among evolutionarily conserved memory systems.

What Is Mentally Represented in Episodic Memory?

The example of WWW memory shows how memories can be encoded in a variety of ways. 'When' could consist of different kinds of temporal information, from the time of day at which an event occurred, how long ago an event occurred, how strong a given memory is, to which events preceded and which followed a particular event (Figure 3). When monkeys (*Macaca mulatta*) were presented with trial-unique sequences of images, it was the number of intervening items, rather than passage of time *per se*, that most strongly determined memory for the order of occurrence [30] (Figure 2). Honeybees used circadian timing in a WWW memory test, perhaps because they are obligate nectar feeders and nectar availability follows a robust circadian pattern [31]. Foraging decisions in rats often depend on elapsed time, consistent with the finding that the performance of rats in a WWW task was not controlled by circadian time [25], and in a separate test depended on elapsed time [32]. More recently, however, Zhou and Crystal [33] designed a WWW experiment that prevented rats from using elapsed time to guide behavior and found that under these conditions the behavior of rats was controlled by time of day. Not



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surprisingly, different species under different conditions encode time in different ways, some showing stronger parallels to human episodic memory than others.

Memory Is for the Future

Episodic memory, like other types of memory, evolved not for idle reminiscence about the past but because it promotes adaptive action in the present and future ([5], p. 250). In accord with this view, mental simulations of future events in humans rely on the same neural systems responsible for episodic memory [34]. Interest in the extent to which nonhumans plan and otherwise anticipate the future has grown with the development of studies of episodic memory. Black-capped chickadees [35] and western scrub jays [36] selectively chose which foods to cache so as to have access to foods that will address anticipated motivational states, even when currently satiated on that particular food. In a related task, squirrel monkeys (*Samiri sciureus*) altered behavior in anticipation of future thirst [37]. Researchers have begun to develop prospective memory tests to study planning because prospective memory is proposed to require encoding, retention, and retrieval of an intended future action, as when we remember to buy milk on the way home [38,39].

Recall and Recognition

Humans with episodic memory deficits are dramatically impaired in tests of free recall, in which they are required to recollect and produce, rather than simply recognize, remembered material [2]. Nearly all memory tests used with nonhumans are recognition tests but comparative psychologists have begun to develop recall tests, and measures of recollection, for nonhumans. Several hours after observing food being hidden in an outdoor enclosure, a lexigram-trained chimpanzee (*Pan troglodytes*) spontaneously requested to go outside, indicated which food she wanted to locate by pointing to a lexigram keyboard, and successfully directed a human to the location of the food [40]. In a study paralleling the human ability to recall and reproduce images from memory, rhesus monkeys

Figure 3. Brain manipulations do not directly identify cognitive mechanisms.

The lower panel depicts the fact that manipulation of the brain, such as inactivation of the hippocampus, may impair performance in a given test, such as memory for the order of events. The upper panel indicates that this impairment might be caused by any of a variety of changes in the mental representations responsible for performance. The combination of brain manipulations and sophisticated cognitive testing is required to identify the relationships between brain mechanisms and cognitive representations. As described in the text, different species may encode temporal order differently, making independent tests in different species necessary.

reproduced simple shapes from memory on a touchscreen [41]. Analysis of error patterns in rhesus monkeys indicated the presence of both recollective and familiarity-based memory processes in recognition memory tests

[42]. Recollective processes are associated with episodic memory in humans [20].

Convergence of Cognition and Neurobiology

The most informative and exciting studies of episodic memory combine sophisticated behavioral paradigms that identify what information is mentally represented with neurobiological manipulations or measures that identify the neural bases of performance (Figure 1). The rodent studies of memory for order described earlier are good examples of such studies [10,19]. Episodic memories are often encoded incidentally and remembered when unexpectedly needed [29]. Rats reported correctly whether or not they had recently found food, even under conditions in which they should not have expected a test of memory. Availability of this apparently incidental memory was abolished by inactivation of the hippocampus [43]. As described in the introduction, episodic memory encodes the context, or source, of memories. Rats with temporary inactivation of the hippocampus could no longer remember whether they recently entered the arm of a maze on their own or had been placed there by an experimenter [27]. We have not mentioned many other excellent studies combining important cognitive and functional properties of episodic memory with neurobiology, but have rather used these examples to foreshadow the exciting studies we see ahead.

Gaps and Future Studies

Few cognitive studies of episodic memory in nonhumans have sought to dissociate episodic memory from other types of memory, although it is known that hippocampal lesions dissociate memory for order from familiarity [10]. In particular the distinction between semantic and episodic memory has not been extensively developed in nonhumans. Performance in memory tests requires at least two kinds of knowledge. The first is reference memory of the 'rules of the game', such as that food can be found at the end of the arms of a maze or that food can be earned by selecting the image seen most recently. The second is often called 'working memory' and is memory for what has happened recently,

such as which maze arms have been visited or which image was seen at the beginning of the current trial ([5], p. 216). Reference memory has properties of human semantic memory, but the relations between human and nonhuman semantic memory have not been the focus of anything like the effort devoted to the study of episodic memory. It is well-known in humans that no memories, even episodic memories, are simple records of the past. Instead, memories result from reconstructive processes, including interactions between semantic and episodic memory [44,45]. We often infer when our episodic memories were formed by reference to semantic knowledge, for example by reasoning that we must have conversed with our colleague two days ago rather than yesterday because we were out of town yesterday. To our knowledge, no studies of episodic memory in nonhumans have directly addressed the extent to which nonhumans process episodic memories as embedded in structured sequences of events analogous to humans' use of calendars and routines.

Some of the most comprehensive and exciting behavioral data on episodic memory has come from studies of birds [8,24] but there are no studies to our knowledge that directly assess the neurobiology of episodic memory in birds using lesion studies, physiological mapping, or neurophysiology. This gap may be due in part to the difficulty inherent in evaluating the role of the hippocampus in WWW memory, given the well-established role for this structure in spatial memory in primates [46], rodents [47], and birds [48]. It is difficult to distinguish a deficit in episodic memory from one in spatial memory in any behavioral design with a spatial component. This difficulty highlights the need to avoid circular reasoning based on neurobiology alone, for instance concluding that because a particular behavioral performance is dependent on the hippocampus, it necessarily involves episodic memory. Instead, it is critical to determine the cognitive representations that control behavior in a given test, and which components of this represented information are lacking following hippocampal removal, for example.

Comparative and evolutionary studies should focus on differences among species at least as much as similarities, yet within comparative psychology and neurobiology it is common to emphasize similarities. Identifying differences, or specializations, in episodic memory between species can allow testing of hypotheses about the evolution of memory. For example, highly social species may have evolved episodic memory that is especially sensitive to the precise social context in which memories were formed, enabling sophisticated social behavior. By contrast, food-storing birds that cache and recover perishable foods may be especially sensitive to the temporal context in which memories were formed. Only comparative studies, conducted with a broad conception of what episodic memory is, can identify such differences if they exist.

Most modern taxonomies of human memory make a fundamental distinction between memories about which we are aware (declarative or explicit memories) and memories that are unconscious (non-declarative or implicit [49]). Human episodic memories are explicit. Studies of metamemory in nonhumans, in which subjects show that they 'know when they know', suggest that at least some memories in nonhumans are also explicit. For example, monkeys and apes chose to take memory tests in which they were likely to answer correctly but declined memory tests they

were likely to fail. Some nonhumans also selectively seek information only as needed before completing memory tests (reviewed in [50]). Metamemory tests have not yet been combined with studies of episodic memory in nonhumans, but such approaches might be useful.

Conclusions

Advances in our understanding of episodic memory depend on establishing robust dissociations between memory systems based on the neurobiological systems serving memory, the aspects of events mentally represented, and in the kinds of transformations represented information undergoes in the generation of behavior. As these characterizations develop, we will be better able to compare and contrast these systems across species, and to describe the way these systems have likely evolved. By better understanding functional differences in memory among species we will better know what episodic memory is. This knowledge serves the basic science goal of understanding the autobiographical memories that constitute our sense of self, and the more practical need to appreciate which animal models best capture which aspects of episodic memory for biomedical research. We likely will never have satisfactory answers to questions about the phenomenology of memory in nonhumans, but we are making great strides in understanding what features of events are represented, where in the brain, now.

Acknowledgments

Preparation of this manuscript was supported by the National Science Foundation (grants BCS-0745573; IOS-1146316), the National Center for Research Resources P51RR000165, the Office of Research Infrastructure Programs/OD P51OD011132, and the National Institute of Mental Health (grant R01MH082819). We also thank Tara Dove-VanWormer, Jessica A. Joiner, and Benjamin M. Basile for help with photographic images.

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