

Is episodic memory uniquely human? Evaluating the episodic-like memory research program

Sarah Malanowski¹

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Abstract Recently, a research program has emerged that aims to show that animals have a memory capacity that is similar to the human episodic memory capacity. Researchers within this program argue that nonhuman animals have episodic-like memory of personally experienced past events. In this paper, I specify and evaluate the goals of this research program and the progress it has made in achieving them. I will examine some of the data that the research program has produced, as well as the operational definitions and assumptions that have gone into producing that data, in order to call into question the ultimate value of the episodic-like memory research program. I argue that there is a gap between the claims that the research program makes and the data it uses to support these claims, and that bridging this gap is essential if we want to claim that human episodic memory has a meaningful analog in animals. I end with some suggestions of how to potentially fix these problems.

Keywords Episodic memory · Episodic-like memory · Comparative psychology · Comparative cognition

1 The episodic-like memory research program

Human beings possess a form of memory (episodic memory) and a form of consciousness (autonoetic consciousness, or “autonoesis”) that no other animals do. Thus, the thesis is that these two aspects of the mind are unique in humans, in the sense that the mental capacities that define them do not exist in quite the

✉ Sarah Malanowski
smalanowski@wustl.edu

¹ Philosophy-Neuroscience-Psychology Program, The Department of Philosophy, Washington University in St. Louis, One Brookings Drive, St. Louis, MO 63130, USA

same full-fledged form in other species. They do not exist in insects, in birds, in mice or rats, in cats, dogs, and not even in gorillas and chimps (Tulving 2005, p. 5).

The capacity for episodic-like memory is unlikely to be unique to humans and food-storing birds, and is probably important for survival in a number of animals (Clayton et al. 2001, p. 1490).

The above quotes represent a recent debate in the study of episodic memory: whether or not episodic memory is a kind of memory that is unique to humans. Episodic memory is typically thought of as the memory system that “makes possible mental time travel through subjective time, from the present to the past, thus allowing one to re-experience, through auto-noetic awareness, one’s own previous experiences” (Tulving 2002). Because episodic memory is considered to be responsible for the distinctive feeling of remembering one’s own past experiences, it has been commonly thought of as a mental capacity that is unique to humans (Tulving 2002; Suddendorf and Corballis 2010). However, a research program, pioneered by Clayton and Dickinson’s (1998) work on scrub jays, has emerged, claiming that there is evidence that non-human animals also possess a capacity to remember personal experience, a capacity for *episodic-like memory*.¹

The study of episodic-like memory is meant to separate the phenomenological and behavioral components of episodic memory. Researchers of episodic-like memory believe that episodic memory can be studied using purely behavioral methods, and so argue that it can be studied in nonhuman animals. Episodic-like memory is most frequently argued to have been demonstrated when an animal shows that it remembers the *what, where and when* content of a specific past experience.

Because of the prevalent thought that episodic memory is a uniquely human capacity, much of the work done within the episodic-like memory research program has been work that aims to show that nonhuman animals do, in fact, possess a capacity for memory of personally experienced past events²—a capacity that is similar to human episodic memory. However, an important question that I think needs to be considered in regards to the episodic-like memory research program is what exactly the connection between episodic-like memory in nonhuman animals and episodic memory in humans is supposed to be. This question is ultimately tied to the value of the research program—what is it that studies of episodic-like memory aim to conclude from their results.

¹ The “like” in “episodic-like memory” is meant to capture a departure in the method of studying episodic memory: in humans, much work has been focused on the phenomenological aspect of remembering one’s own past (what it feels like to remember a past experience), but the episodic-like memory research program claims that episodic memory can be studied behaviorally, without needing to include the phenomenology. This divorce with the typical way of studying/thinking about episodic memory allows the research program to study episodic memory in animals, who cannot uncontroversially report on what their experiences feel like.

² It should be noted that by “personally experienced past events” here I simply mean memory of an event that happened in the animal’s personal past—that is, the event happened to the animal, or involved the animal in some way. A memory that involves, in Suddendorf and Busby’s words, mental time travel, or the reliving of past events. The animal need not be a person or have any kind of robust sense of self.

A few of the goals that can be found stated throughout the literature are: (1) To find evidence that episodic memory is not unique to humans (e.g. Clayton et al. 2003). (2) To determine what the underlying neurobiological mechanisms of the episodic memory system are (how episodic memories are formed and retrieved) in humans (e.g. Morris 2001). (3) To develop possible animal models for studying episodic memory loss/decline (as in Alzheimer's related amnesia) (e.g. Fouquet et al. 2010). (4) To create methods for studying episodic memory in nonlinguistic humans (i.e. young children) (e.g. Clayton and Russell 2009; Russell et al. 2010). Together, these aims suggest that research in the program assumes that episodic-like memory in animals will turn out to be supported by biological mechanisms that are similar to those underlie episodic memory in humans. From this, then, we can formulate two major goals for the episodic-like memory research program:

- (1) Provide evidence that nonhuman animals have the ability to remember personally experienced past events (that animals have episodic-like memory).
- (2) Create animal models of episodic memory, which will allow for easier study of the biological mechanisms of episodic memory and the development of treatments for episodic memory loss.

The ultimate value of the episodic-memory research program lies, I think, in (2), though, of course, goal (2) requires that the program has done a good job with goal (1). The state of the research program is now moving more towards the second goal of using animals to study human episodic memory (Morris 2001; Salwiczek et al. 2010), but it is important to note that moving from (1) to (2) requires establishing another kind of evidence: evidence that the episodic-like memory studied in nonhuman animals *works* in a way that is similar to the way human episodic memory works; that is, that episodic-like memory and episodic memory are actually produced by biologically similar mechanisms. So we can formulate a necessary in-between goal for the research program:

- (1.5) Provide evidence that episodic-like memory in animals works in a way similar to the way in which human episodic memory works.

I think that the episodic-like memory research program has failed to accomplish (1.5), due in large part to the evidence used to establish that animals have episodic-like memory. Without establishing (1) and (1.5), it is hard to see what the value of the episodic-research program is, because its major purpose is to make comparative claims about human and nonhuman episodic memory. In this paper, I want to analyze how well the research program is doing in terms of these goals by discussing some of the data, operational definitions, and assumptions that are part of the research program. I will examine two major issues with the episodic-like memory research program: the failure to distinguish between what an animal can do in a task and what it actually does in the wild, and the problems with translating an operational definition of a human mental capacity to an operational definition of that mental capacity in nonhuman animals. In doing so, I hope to draw attention to a gap between the claims made in this research program and the data/tasks used to support these claims, a gap that I argue ought to

be considered if we are to draw meaningful conclusions from episodic-like memory studies.³

2 Episodic-like memory: the data

The episodic-like memory research program is concerned first and foremost with establishing that animals have memory for personally experienced past events, since all other claims that are made about episodic-like memory depend on animals actually having episodic-like memory. It is thus crucial that the data produced by the research program really show what they are claiming to show. Because of the importance of establishing the existence claim, I want to start by going through one of the most cited experiments in the episodic-like memory research program, and highlight some of the issues that arise which call into question drawing the inference that these animals are demonstrating a capacity similar to human episodic memory. Each experiment will, of course, need to be evaluated on an individual basis, but my hope is that the issues I discuss here will highlight some of the more general problems that any experiment aiming to demonstrate the existence of an episodic-like capacity will have to address.

Clayton and Dickinson (1998) initially put forth the possibility that we can study episodic memory in animals by focusing on what kinds of information animals are able to encode. They chose scrub jays as their experimental animal because scrub jays naturally store excess food so that they can recover and eat it in the future, a behavior known as caching. Clayton and Dickinson were interested in studying *what* the scrub jays are able to remember when it comes to caching: it is clear that they remember where they cache food, since they are successfully able to recover at least some of the food that they cache, but it was not clear whether the content of the memory incorporated more than spatial information. Clayton and Dickinson thus tested whether the birds' caching memory was sensitive to other kinds of content, namely *what* was cached and *when* the caching was done. In order to do this, they gave the birds two different types of food to cache and manipulated the consequences of recovering each particular kind of food: recovering wax worms was deemed to be more rewarding than recovering peanuts, because wax worms are the birds' preferred food, and so the birds should preferentially search the places in which they cache the worms if their memory is sensitive to *what kind* of food has been cached. However, successful recovery of the worms was also made to be contingent upon the amount of time that had passed between caching and recovery—the wax worms were replaced by decayed (therefore inedible) wax worms by the experimenter if a long period of time passed (124 h, in this experiment) between caching and recovery, and so, if the birds' memory also

³ Although my focus here is on comparative research on episodic memory specifically, I think many of the points I raise can be applied to other sub-fields of comparative psychology. As I will end up arguing, many of my criticisms stem from the way that the episodic memory phenomenon is described (in both animals and humans), and how this description matches up with the particular goal of showing that the episodic memory system works, mechanistically, in a similar way across species. Thus, I believe my criticisms probably extend to sub-fields that have similar goals and have similar problems with phenomena definition. Although I think my criticisms can be applied outside of the comparative episodic memory program, I also think it is important to individually examine each sub-field, its goals, and its data.

contained a representation of *when* the food was cached, the birds should only search for places in which worms were hidden if the worms were not cached very long ago (4 h, in this experiment). The birds could only cache in one side of the tray at each time period, so they also had to remember *where* each kind of food was cached.

One group of scrub jays was thus taught that the worms would decay and become inedible after a period of time (the Degrade group), while a control group was not taught such a contingency (the Replenish group). Birds in both groups had two caching periods: one, 124 h prior to recovery (long interval), and the other 4 h prior to recovery (short interval) and during each caching period the birds were given a caching tray with two sides, with only one side (left or right) available to be cached in at each particular time period. At each time period, the birds were given either peanuts or worms to cache, so the birds ended up caching one kind of food in one side of the tray at each time interval. Clayton and Dickinson then measured how many inspections the birds made to each side of the tray. If the birds are able to form memories about the caching event that include information about not only where they cache, but also what they cache and when they cache it, then the birds that learn that worms become inedible over time should search for peanuts and not worms if they cache worms at the long time interval (because the worms have decayed), and they should search more for worms if they cache worms in the short interval (because the worms are fresh, and the birds prefer worms).

The data were in line with the predictions: the birds in the Degrade condition (i.e. the ones that learned that the worms decay) searched the peanut trays significantly more times than they searched the worm trays on trials in which they had cached the worms a long time before recovery, and they searched for these worms significantly less than birds that never learned that worms decay. Based upon these results, Clayton and Dickinson argue that during recovery, the birds are recalling what food they cached (worms or peanuts), where they cached it (left or right side of the tray), and when it was cached (long or short time interval), and thus that the birds demonstrate having episodic-like memory.

There are, however, a few ecologically-based reasons to resist Clayton and Dickinson's interpretation of their results. Caching is a natural behavior in scrub-jays, and so, if scrub-jays can and do⁴ utilize an episodic-like memory capacity, we should see this more or less reflected in their natural caching behavior in the wild. That is to say, we should see wild birds showing signs of encoding what–when–where content, and we should see a reason that would actually *need* to have this kind of information in order to give them some kind of advantage (like being able to eat more food).

However, it is not clear why, ecologically speaking, scrub jays would need to represent the “what” content of the caching event. *Prima facie* one may think it would

⁴ I say “can and do” utilize here, but I think there is an important distinction to be made between being able to use some capacity and actually using that capacity, which I will discuss later in this paper. However, it is not clear to me whether Clayton and Dickinson (or the other researchers within the episodic-like memory program) are arguing that scrub jays regularly do use episodic-like memory (like in their daily caching behavior in the wild), or simply that they are *able* to form episodic-like memories under experimental conditions, but perhaps do not do so normally. To preview upcoming arguments, I think what really matters is the “do” in the can/do distinction, and that it doesn't make much ecological sense to say that scrub jays are using episodic-like memories—that is to say, that they are not fulfilling the “do” condition.

be evolutionarily beneficial for scrub jays to be able to remember “what” content because it could allow the birds to assess the risk/reward of caching certain types of food: worms might provide more energy (higher reward) but decay faster (greater risk) than nuts. However, scrub-jays do not appear to need this kind of risk/reward assessment in the wild: although they eat different types of food in the wild and will cache different types of food in an experimental setting, observation of caching in the wild involves either acorns or pine nuts, exclusively, depending on what region the scrub jays are found (Degrange et al. 1989). Thus, it would be unnecessary for the birds to encode what kind of food got cached, because they are always caching the same kinds of food. It also seems to be the case that it is unnecessary for the jays to encode *when* they cache the acorns or pine nuts, as well: because they have a hard shell, these nuts are relatively resistant to spoilage, and so the jays do not really need to know how long ago the nut was stored. This concern is amplified by considering the fact that the jays appear to check nut quality prior to transporting it to the cache site, thus reducing the chance of caching cracked or otherwise defective nuts more likely to spoil.

Another aspect of caching behavior also suggests that scrub jays do not need to encode *when* content. One thing of note about scrub jay caching behavior is that the jays will often recover a cached acorn and then rebury it without eating it. Reburying behavior is extremely frequent (greater than 90% of acorns that are recovered are reburied) in the fall months, with nearly all of the acorns observed to be uncovered during this time being subsequently reburied (Degrange et al. 1989). Degrange et al. (1989) have suggested that reburying “permits jays to assess the quality of their stores and reacquaint themselves with their locations” (p. 354). If this is the case, then it appears as though the frequent reburying behavior would render representation of the *what* and *when* content of the cache to be unnecessary for scrub jays. Scrub jays also only recover about one third of the approximately 8000 acorns that are cached during a 1 year season (Balda and Kamil 2006). If they were operating with a true episodic-like memory system, we might expect that they would cache less with a greater rate of recovery—that is to say, the system would be expected to be overall more accurate and efficient, since it is not clear what other benefit the jays would receive from remembering the caching event as an actual episode.

It also does not seem to be the case that the scrub jays would want to utilize an episodic-like memory system to reduce either inter- or intra-species theft, a possibility that is suggested in Clayton and Dickinson (1998). Theft may have been a *prima facie* reason to think that the scrub-jays would benefit from remembering when they cached their food: the longer the food has been cached, the more likely it is to be stolen, and so encoding when the food was cached would allow the birds to recover their caches at an optimal time. However, scrub jays are territorial, and they share their territory with a cooperative breeding mate and “helpers” that are offspring from previous breeding seasons (Woolfeden and Fitzpatrick 1990). Thus there is little threat of theft from other scrub jays. Additionally, there is also little threat of theft from other bird species, because the other species that eat acorns and pine nuts do not typically forage on the ground, where the jays cache.

Consideration of the overall behavioral patterns and habitat of scrub jays suggests that these birds do not need to encode *what* and *when* information about their caches: the environment and the rest of their behavioral repertoire contains all the information

that they need for successful caching behavior. Thus, even if it is the case that Clayton and Dickinson are correct and their scrub jays are in fact forming episodic-like memories (i.e. memories that contain representations of what, when, and where information), exercise of an episodic-like memory capacity appears to be constrained to experimental settings, because scrub jay behavior in the wild suggests that episodic-like memories are not being formed. In other words, assuming that Clayton and Dickinson's interpretation of their results is correct, the authors have only demonstrated that the scrub jays are able to form episodic-like memories, and not that the formation of episodic-like memories is something that the species regularly does.

3 The difference between “can” and “do”

I think this distinction between what the birds (and any other species studied in this research program) can do versus what they actually do has important implications for how we should interpret the results of episodic-like memory studies. Recall that one of the goals of the episodic-like memory research program is to demonstrate that non-human animals have a memory capacity that is similar to the episodic memory capacity found in humans. The research program's strategy for doing this involves stripping away the phenomenal components of episodic memory so that we are left with a capacity whose existence can be inferred through behavior alone. As I argued above, the behaviors required to make an inference about an episodic-like memory capacity are only exhibited in the case of the scrub jays in the context of an experimental task, so our inference about their memory capacity is dependent on the fact that they *are able* to use episodic-like memory to do the experimental task. But, then, the question becomes, how do we establish that the animals are actually using an episodic-like memory system to do the experimental task?

Here lies the key problem: there are many ways to do a task. If the animals are not actually using the capacity regularly, then it is hard to get an argument that they are able to do it in the context of an experimental task off the ground, because it is very difficult to rule out that they are not producing the behavior required by the task in a way other than the one that is supposedly being tested. If they only appear to use the capacity in experimental circumstances, then it does not seem plausible to infer that they actually have a capacity for episodic-like memory; instead, it seems likely that the animals have found other ways to do the task. Good experimental design will, of course, try to control for the possibility of alternative ways of producing the behavior, but I think this is very difficult to actually do in practice, given the huge amount of training that is typically associated with animal studies. For example, in the study described above, the scrub jays used had been involved in two other studies, each with its own training and pre-training periods. We should thus assume that the birds have learned that there are rewards to be gained from learning how to perform the tasks that the experimenter wants them to perform. It is therefore not surprising that they learn how to do the tasks with some rate of success, but, because of the sheer amount of training the animals receive, we cannot infer from the fact that they are doing the task that they are doing the task in the way we think they are doing it. In other words, we cannot make a good inference from their behavioral performance to the cognitive processes underlying the

behavior, because there are many different cognitive processes that can produce similar behaviors. It need not be an episodic-like memory capacity that allows the animals to perform the behavioral task; instead it can be any number of cognitive processes that the birds *do* possess redeployed to complete the task.⁵

An argument given by Povinelli and Vonk (2003) in regards to the study of theory of mind in primates is, I think, relevant here: because we are not behaviorists, we can help ourselves to all sorts of mental representations (representations of what, where, and when, for instance), without needing to jump to the conclusion that the animals are representing episodes from their past. The options are not simply stimulus response chain or full-blown episodic system—there is an array of options between these two that invoke mental representations, just not in the same way as the human episodic memory system. The birds could be utilizing rather sophisticated representations of what, when, and where, but this does not imply that they have a memory system that is anything like the human episodic memory system.

It is easy to see how this worry about inferring cognitive processes from performance on the behavioral task is intensified by considering the can/do distinction: the fact that the animals *can* do the task in an experimental setting but do not regularly *do* behaviors in the wild that suggest they are using an episodic-like memory capacity makes the inference that the animals are using such a capacity in the task much more implausible. If we can already, because of worries about overtraining and the like, doubt whether the behavior actually reflects the cognitive process/capacity in question, and then it turns out that the animals do not appear to or need to use such a capacity in the wild, then it seems like we are not justified in drawing the conclusion that the animals are using this capacity during the experimental task.

Although the above discussion has centered around one study within the episodic-like memory research program, it highlights some concerns that each study of episodic-like memory will have to address in order for any plausible conclusions

⁵ One way of overcoming the worries about overtraining is to design tasks that involve only one training period. Object recognition tasks are one such design. These tasks take advantage of rodents' natural exploration of novel objects and tendency to explore novel objects more than familiar ones. This task design can be applied to study episodic-like memory in rodents in a way that does not involve overtraining. For example, Dere et al. (2005) designed a task that involved exposing mice to two different sets of novel objects that were each arranged in a particular spatial layout. Both sets of objects were presented once, with a time delay between each presentation. One set of objects was thus more recently presented than the other set. The test trial involved an array that included two of each type of object (four objects total), with all but one in the original spatial position they were presented in. Mice spent more time exploring the older items than the more recent items, and more time exploring the old object that was out of place than the old item that was in place. The authors argue that this pattern of exploration suggests that the mice have episodic-like memories of their initial encounters with the objects because their more frequent exploration of the older, displaced object shows that they remembered what the object was, when it was presented (longer ago in time), and where it was presented—thus, it is a demonstration of episodic-like memory from only two training trials. Although this experimental design overcomes overtraining worries, it comes with its own set of concerns—for instance, the fact that the mice could be making judgments based on familiarity (stronger memory trace for more recently encountered set of items), rather than explicit recall, along with the assumption that novelty can be ranked, and that this ranking corresponds to different amounts of exploration. Most importantly though, overtraining is only one concerning feature of episodic-like memory tasks, and this experiment does not overcome the worry that the animals are not demonstrating a type of memory that works similar to human memory, and the worry that demonstrating *www* memory does not mean that the animals remembered a personally experienced past episode. I discuss these worries more below.

about the existence of an episodic-like memory capacity in their choice species to be drawn. These concerns are: (1) How much are the animals trained? If the animals are over-trained, they can develop their own methods for doing the task that look nothing like the methods humans use.⁶ (2) How well do the animals actually do the task? If robust memories that integrate what, when, and where information actually are formed, then we should expect very high accuracy on tasks that appear to require encoding of this information. (3) Do the animals actually use/need to use an episodic-like memory capacity in the wild? If not, than a more plausible explanation of experimental results is that they have developed a different way of doing the task that does not utilize an episodic-like memory capacity. Note that these concerns arise largely because of the particular goals that the research program has—these studies aim to show that the animals are completing the task using the same mental capacity that humans use to complete the task. This inevitably restricts the set of mental capacities that are considered to possibly underlie the behavior: if the animal displays a particular behavior, then it is argued to have a specific human-like mental capacity, when, realistically, there are many other mental capacities that could potentially produce the same behavior.

The above discussion highlights the issues with the first aim of the episodic-like memory research program, demonstrating the existence of episodic-like memory in nonhuman animals. Assuming that the research program overcame these worries that come along with attempting to show that nonhuman animals have an episodic-like memory capacity (perhaps by creating extremely well-designed experiments that did not rely on overtraining the animals), would we then be able to create a good model of human episodic memory (the second goal of the research program)? The answer to this question relies on how closely the episodic-like memory system in animals matches the episodic memory system in humans, and I want to now argue that we have reason to doubt that that match would be very good at all.

4 Operational definitions

The first objective of the episodic-like memory research program is to establish that nonhuman animals actually have episodic-like memory. In order to study episodic memory experimentally, we, of course, need some kind of operational definition of episodic memory—a way of determining when an experimental subject is demonstrating episodic memory. The operational definition of episodic-like memory that is embraced by the research program thus plays a crucial role in the success of the research program: whether or not the field finds evidence for episodic-like memory depends on how they define episodic-like memory. As we will see, though, the operational definition that is chosen can impede (and has, in fact, impeded) progress in showing

⁶ Although, as Felipe de Brigard has noted to me, a similar problem can arise within human populations as well—different human populations may have different ways of doing a task, even their performance is identical. However, this highlights the importance of having an idea of just how, mechanistically, the task is performed. If we know something about the neurobiological workings underlying task performance, we are in a better position to say that two populations—be it two human populations or a human and animal population—are performing the task in the same way.

that episodic-like memory and episodic memory work in similar ways, biologically and psychologically.

In humans, one of the prevalent operational definitions of episodic memory involves reports of subjective experiences of remembering past experiences (Tulving 2002). In animals, however, a different operational definition is needed, since there are no uncontroversial ways of obtaining subjective reports of their experiences. And so, the research program has, for the most part, settled on an operational definition based on the content of the memory—the what–where–when information that is encoded. It is important to remember why the program developed the operational definition of episodic memory that it did: so it could pick out whether animals have the capacity for episodic memory or not. That is to say, when we see an instance of what–when–where content being encoded, we want to be able to infer that the animal has the episodic-like memory capacity. This means that meeting the content criteria (i.e. demonstrating knowledge of what–where–when information about the event) needs to be sufficient for episodic-like memory. The what–when–where condition is also usually considered necessary when it comes to demonstrating episodic-like memory experimentally: if one of the conditions is not met by the animal during the experiment (for instance, if the animal does not demonstrate that it knows when the event occurred), then an inference about episodic-like memory cannot be made.

However, there is a major problem with making what–when–where knowledge necessary and sufficient for episodic-like memory, and that is the fact that what–when–where knowledge is neither necessary nor sufficient for human episodic memory. For human episodic memory, the crucial factor is that the memory is of something that happened in the subject's personal past. I can demonstrate what–when–where knowledge of the first manned moon mission, but I simply cannot have an episodic memory of it because I was not alive in 1969 to experience it. I can remember all sorts of details about the first manned moon landing, but none of these memories will qualify as being episodic memory of the moon landing itself—they are not sufficient for episodic memory. Similarly for the scrub-jays, it seems strange to attribute to them episodic memory if their memory is not actually of their past experience. The scrub jays may have the memory of exactly when in the past the food was cached, but unless the memory includes content about the scrub jay's experience of caching the food itself, the memory does not appear to be genuinely episodic. I can remember where my keys are and when they were put there without needing to remember the experience of me putting my keys there last night. On the flipside of this, it seems as though I can have an episodic memory of my key placing experience without remembering when the experience occurred, so having full what–when–where (www) knowledge is not necessary for having an episodic memory of my experience. In other words, knowing what my keys are, where I put them, and how long ago I put them there is neither necessary nor sufficient for an episodic memory of putting my keys down.⁷

⁷ The fact that remembering what–when–where information does not entail remembering a past episode has also been noted by Suddendorf and Busby (2003). They argue that if we characterize episodic memory as www memory, then there is no implication that the phenomenon of episodic memory involves remembering a past episode. I return to this idea in the final section of this paper.

Furthermore, in general, content by itself is an odd sufficient condition for establishing that we are observing a particular kind of thing (episodic-like memory, in this case). If I am holding a book and I want to know if I am holding a ghost story, merely opening the book and seeing a picture of a ghost is not, strictly speaking, sufficient evidence for the book being a ghost story. The book is certainly, at least in part, about ghosts, but what makes a ghost story a ghost story (and not, for instance, a guide to drawing ghosts) is the relation between the content and the way these relations are organized (e.g. the ghost scaring the people in the abandoned house). Similarly for episodic-like memory, merely demonstrating the what, when, and where content is simply not sufficient for demonstrating anything episodic-like—what makes something an episode (or like an episode) is the relation between the what, where, and when. Demonstrating that integration of the content in a particular way has occurred is crucial for being able to plausibly say that animals have a capacity that is anything like human episodic memory. However, tests of episodic-like memory in pigeons suggest that, although pigeons can successfully do an episodic-like memory task by encoding the what, when, and where information about test items, the pigeons are not binding this information into a single memory—instead, the pigeons encode what, when, and where information independently (Skov-Rackette et al. 2006). These findings suggest that, even if animals can be uncontroversially shown to have encoded what, when, and where information about an item or event, we would still need further evidence to show that this information has been encoded in a way that is similar to the integrated way a human episodic memory is encoded, in order for animal episodic-like memory and human episodic memory to be similar processes.

The fact that the operational definitions of episodic-like memory do not appear to capture a capacity that is all that similar to human episodic memory is worrisome given the goals of the research program: if the capacity that is being studied is actually quite dissimilar from the capacity of interest, then it is unlikely that there will be similar biological mechanisms underlying them. Other operational definitions of episodic-like memory have been developed in order to try to test for a capacity that is more similar to human episodic memory, though it appears as though the majority of the work in the field, especially the work that is concerned with developing an animal model of human episodic-like memory, uses the “what–when–where” operational definition (Zhou and Crystal 2009; Crystal 2010).⁸ As noted above, this definition of episodic-like memory fails to capture what appears to be the distinguishing feature of human episodic memory. Schwartz and colleagues have attempted to overcome this problem by adopting a different operational definition of episodic-like memory. Rather than demonstrating that an animal at the time of the test knows what, where, and when information about a past event, Schwartz et al. use an operational definition of episodic-like memory that attempts to capture the “palinopsychy” (“past orientation”) that human episodic memory involves: the animals need to report on a past experience, rather than report on current knowledge, in order to demonstrate episodic-like memory. The relevant distinction here is similar to that between knowing my keys are on the table versus remembering the event of placing them there—I can have knowledge of

⁸ Along with permutations of “what–when–where”, including “what–where” and “what–when” (see Allen and Fortin 2013 for brief review).

where they are without remembering putting them there. Schwartz et al. argue (rightly so) that it is the *remembering* component that defines human episodic memory, and so remembering should be a feature of an operational definition of nonhuman episodic-like memory as well. They have tested their palinoscopic conception of episodic-like memory primarily using a task that requires the animal subjects to “report” on which events happened in their past. Their research using this more demanding operational definition has focused, perhaps unsurprisingly, on primates, particularly on one gorilla, King, living in protected primate habitat. The basic experimental design for the tests done on King involves having King experience some event (e.g. receiving food from a particular experimenter, seeing a novel object), then giving him several photographs a day later, one of which depicts the event/item experienced, which he then has to choose between. Choosing the “correct” photograph (the one with the experienced item) is interpreted as reporting and remembering a past experience.⁹

I mention this alternative operational definition of episodic-like memory because it appears to run into similar problems as the “what–where–when” content definition, despite its attempt to more closely mirror the human phenomenon. The content-based operational definition is problematic because it doesn’t capture what we really mean by human episodic memory, but it is also problematic because animals can fulfill it without having a memory system that is similar to a human episodic-like memory system. The palinoscopic operational definition attempts to combat the first problem by focusing on reports of past experiences, but I believe that it still fails to overcome the second problem. Insofar as the experiments on episodic-like memory that take on the palinoscopic operational definition are trying to demonstrate a memory system that is similar to the human episodic memory system, they ultimately fail: King the gorilla only needs to recognize which events have occurred in his past in order to complete the task—he does not need to actually recall these events. His responses can be based entirely on the *familiarity* of the stimuli on the cards. This is important, because there is a clear distinction between familiarity and recall that is made in the literature on human memory—what is known as the remember/know distinction. Although there is considerable debate over just what this distinction amounts to (see [Yonelinas 2002](#) for review), empirical evidence suggest that recalling/remembering an event or item is different behaviorally and neuropsychologically than recognizing an event or item as familiar. Because most researchers agree that remembering requires different processing than knowing, the fact that King the gorilla “knows” which event occurred in his past does not lend support to the claim that gorillas have a memory system (or a memory process) that is similar to the one humans use when remembering events.¹⁰

⁹ Other variations of this experiment have attempted to capture both the “remembering” aspect of episodic memory and the “what–when–where” content aspect. For instance, in one experiment King had to temporally order photographs of foods he had recently eaten ([Schwartz et al. 2005](#)).

¹⁰ The relationship between the remember/know distinction and the episodic/semantic distinction is not entirely clear cut: although the remember/know paradigm was originally used to test hypotheses about differences between the episodic and semantic memory systems ([Tulving 1985](#)), other researchers who study the remember/know distinction have not committed themselves to the claim that remembering and knowing are done by different memory systems, like Tulving has. Instead, most argue for more subtle distinctions in processing between the two kinds of remembering involved in remembering and knowing.

In this section, I have argued that the prevalent operational definition of episodic-like memory does not leave the research program in a position to achieve its goals of showing that nonhuman animals have a memory system that is similar to the human episodic memory system, because animals can display episodic-like memory behavior under this definition without this behavior being very similar to human episodic memory behavior. Furthermore, attempts to alter the operational definition to make it more in line with the human phenomenon have still failed to demonstrate that animals have an episodic-like memory system that *works* like the human episodic memory system. Showing that the underlying processes and mechanisms, and not just the behavior, are similar across human episodic memory and nonhuman episodic-like memory is essential, given the research program's aim to show that an episodic memory system is conserved across species. But many of the current operational definitions of episodic-like memory are ill-suited to do this, by design: in order to make episodic memory researchable in nonhuman animals, the research program has focused itself on the behavioral aspect of episodic memory, but, as we have seen, demonstrating episodic-like memory behavior is simply not sufficient for demonstrating an actual episodic-like memory system. In order to draw a comparison between human and animal episodic memory, the operational definition should suggest something about the way the system works.

There are thus many problems that arise when we try to get clearer on what is and what should be required of an operational definition of both episodic-like and episodic memory. Many of these problems arise because current operational definitions do not make any commitments to the workings of episodic-like memory, and establishing that episodic-like memory utilizes a neuropsychological system that is similar to the human episodic memory system is essential to the research program's success.¹¹ However, these problems presuppose that there is a human episodic memory system that a nonhuman episodic memory system can be similar to—that is to say, this discussion about whether or not the operational definition of episodic-memory sufficiently captures the important aspects of human episodic memory presupposes that there is such a distinct thing as human episodic memory. So far, we have focused on some of the problems with the study of episodic memory in animals, but I want to now discuss a criticism of the episodic-like memory research program that arises from the human side of the study of episodic memory.

5 How should we characterize human episodic memory?

The entire preceding discussion of the study of episodic-like memory in nonhuman animals and its relation to human episodic memory has been predicated on the assumption

Footnote 10 continued

Regardless of whether or not the remember/know data support a claim about memory systems, though, it is still the case that if there is such a thing as a distinct episodic memory system, then the remembering involved in episodic memory is most likely going to involve the remembering processes that are studied in remember/know paradigms, and so data claiming to demonstrate episodic-like memory should show that remembering processes, rather than knowing processes, are being used.

¹¹ Some authors have recently tried to operationally define episodic-like memory with an eye specifically towards the neuropsychological mechanisms that underlie it. I return to these definitions in Sect. 6.

that there *is* an episodic memory capacity in humans. However, there is some reason to doubt this claim, which puts the episodic-like memory research program on even shakier ground—after all, if there is no distinct episodic memory system in humans, then, of course, attempting to find a similar system in nonhuman animals is a nonstarter and the episodic-like memory research program has problems that extend way beyond operational definitions and ecological considerations. Closely examining skepticism concerning human episodic memory is well beyond the scope of this paper, but I want to highlight a few points that directly pertain to the study of episodic-like memory in nonhuman animals.

Much of the criticism that has surrounded the view that episodic memory is a distinct system has focused on the distinction between episodic and semantic memory (or, more specially, the lack of a distinction). For example, [Glenberg \(1997\)](#) has argued that there is no distinction between the episodic and semantic memory systems, and that the appearance of such a distinction has arisen because of the differences in the tasks that are used to assess semantic and episodic memory, which result in different information being processed which is then used in different ways in each of the types of tasks. In other words, the difference between episodic and semantic memory can be found in the task conditions, not in the systems used to do the tasks. This is similar to a concern that we saw with the episodic-like memory literature, in which there is a gap between the task performance and the inferences that we make about memory systems. Similar arguments have been made against other memory system distinctions as well. For instance, one of the more clear-cut distinctions in memory systems, between that of declarative and procedural memory, has recently been criticized ([Stanley and Krakauer 2013](#)). Stanley and Krakauer have argued that there is no reason to think that procedural knowledge and declarative knowledge come apart in any neat way. Instead, the distinction between the two has been forced into the literature by the task choices that are made and the way the data are interpreted. If they are right and procedural and declarative memory, two kinds of memory that actually appear to be very different, are not separate systems, then it becomes less plausible that the comparatively subtle distinction between episodic and semantic memory is reflected in different memory systems.

In response to these kinds of worries, [Tulving \(2002\)](#) has clarified just what an episodic memory system is: “Episodic memory is a hypothetical memory system. It is not a particular kind of memory task or test. According to episodic theory, there exist few, if any, memory tasks used in the laboratory or the clinic that involve a single memory system. In terms of memory systems, all tasks are ‘multiply determined’” ([Tulving 2002](#), p. 5). The idea here is that it is a mistake to look only at task performance anyway, because no memory task can actually capture the real distinctions between memory systems. Tulving has advocated that we instead look more to biological evidence for a distinct episodic memory system. However, lesion case studies, the backbone upon which the biological argument for the episodic/semantic distinction has been built, still depend on task differences to make the distinction in the first place.

The biological distinction between episodic and semantic memory systems is further complicated by the fact that the two systems are most likely not divided up neatly—they are not split up into, say, two distinct brain regions. Even proponents of episodic memory agree that there is good reason to believe that the “operations of all

memory systems are supported by widely distributed and intricately interconnected regions of the brain” (Tulving 2002, p. 12). Given that episodic memory is likely to involve so many different operations and brain areas, it is not clear the extent to which it even makes sense to say that episodic memory involves a distinct memory system: the purpose of defining systems is often to isolate a particular operation or function in a narrow range of the brain, not the conjunction of many different operations and areas.¹² The phenomena that presumably involve lots of different operations spread across the whole brain are, usually, precisely the phenomena we do not want to say have their own distinct systems—writing a paper or riding a bike, for instance. It is not clear to me that the phenomenon of remembering a past experience is any different in this respect. Granting that episodic memory is a distinct memory system that happens to be comprised of a widely distributed set of operations and brain regions, though, then it seems less likely that such a system is evolutionarily conserved across species—or even that it has evolved in a Darwinian fashion at all. An episodic memory system might be similar to a reading system: a set of existing, distributed operations that we learn to use in a certain way in order to do certain kinds of tasks. The fact that the episodic memory system, if it is a system at all, is only a system in a fairly loose sense makes it hard to make a convincing argument that episodic memory is evolutionarily conserved: the evolutionary conservation of cognitive mechanisms is one of the more compelling reasons for embracing a modularity-based view of cognitive architecture, and the more distributed a cognitive system is, the less modular it appears to be. In other words, a widely distributed episodic memory system is, by definition, not a very modular one, and so not a system we should expect to be conserved across species (especially ones as distally related as scrub jays and humans).

Whatever human episodic memory is—if it is even a distinct memory capacity at all—it is clearly up for debate how best to characterize it. Tulving himself began with a definition of episodic memory that emphasized the type of information processed by the episodic memory system (Tulving 1972), but later moved on to a definition that emphasized the experiential and self-oriented features that differentiate episodic memory from semantic memory (Tulving 2002). Similarly, Suddendorf and Corballis (2007) argue that the core component of episodic memory is mental time travel, the mental construction of specific scenarios in either the past or the future. Meanwhile, other authors attempt to create some distance between human episodic memory and autooetic consciousness—Cheng and Werning (2015), for example, define episodic memory as the representation of a temporal sequence of events that the subject experienced. Importantly, each different characterization of episodic memory will carry with it implications for what neural mechanisms we think are involved. Thus, the definition of episodic memory is important for the comparative program, given that the

¹² Of course, this depends on what we mean by “distinct memory system”. Cognitive systems, including memory systems, are defined by a combination of the information-processing task, the rules of operation, and the neural implementation (Schacter and Tulving 1994; Michaelian 2011). Perhaps episodic memory has its own information processing task with a certain implementation, but if this information processing task itself involves several distinct information processing tasks each with their own implementation, then there is a sense in which episodic memory is made up of several different systems. Just what is the right sense of “distinct system” is up for debate, but I believe it has something to do with what the explanatory goals are, an idea I return to in Sect. 6.

comparative program's major goal is to show that animal episodic memory works in a way similar to human episodic memory.

From this discussion it should be clear that characterizing the phenomenon of interest is a crucial aspect of the episodic-like memory research program. There are a number of different ways we can characterize the phenomenon of human episodic memory. Similarly, there are many different ways we could characterize the phenomenon of scrub jay caching behavior. If we characterize this behavior as “episodic-like memory”, then, of course, we are suggesting that the phenomenon shares something in common with the human phenomenon of episodic memory. However, this might not be the right way to characterize the caching phenomenon—it might not be very similar to human episodic memory at all (even a simplified version of human episodic memory). Thus, it might be better to do as [Suddendorf and Busby \(2003\)](#) suggest and characterize the phenomenon more neutrally as simply “what–when–where memory”, rather than episodic-like memory. Our description of the behavioral phenomenon that we are trying to explain is thus somewhat flexible, and is often times dependent upon our explanatory goals. I have argued here that a major explanatory goal of the episodic-like memory research program seems to be to show that non-human animals have a form of memory that works in a way similar to human episodic memory. This is just one of many possible goals a research program can have, but given that this particular research program has this particular goal, I want to now consider this goal in light of the fact that our description of the episodic memory phenomenon is somewhat flexible.

6 Moving forward: what is the phenomenon?

Up to this point I have been critical of the episodic-like memory program, but some may still, reasonably, see value in pursuing a comparison between animal and human episodic memory. Although I have argued that the prevalent ways of operationally defining episodic memory are not in line with the goals of the comparative episodic memory program, some authors (e.g. [Allen and Fortin 2013](#); [Cheng and Werning 2015](#)) have recently tried to bring neuroanatomical and neurophysiological evidence to bear on these operational definitions. Furthermore, although I have argued above that it is unlikely that there even is a distinct episodic memory system in humans, I understand that this claim is contentious. There are, after all, good empirical reasons and theoretical arguments for thinking about episodic memory as a distinct capacity in humans, and, if we accept these, then there are plausible evolutionary arguments for the conservation of memory mechanisms across species. I certainly respect this position, but, if it is accepted, I think it is important to consider how such a comparative program should proceed in light of the issues I have discussed here.

Above, I highlighted the importance of showing that episodic-like memory in animals works in a similar way, mechanistically, to episodic memory in humans. Certainly one way to bolster any claim that some species has an episodic-like memory system is to show that that species shares some neurophysiological or neuroanatomical similarities with humans within the relevant brain systems or structures and during the relevant tasks or behaviors. This is precisely what some authors have recently attempted to do. For instance, [Allen and Fortin \(2013\)](#) have argued that the system of brain areas that is

involved in human episodic memory is present throughout mammals and birds. Furthermore, they argue, neural mechanisms for processing and integrating information about *what*, *where*, and *when* are present in this brain circuit and are similar across mammals (and, perhaps, birds)—other animals have neural mechanisms that work, mechanistically, like the neural mechanisms involved in processing and integrating what–when–where information in the human brain. Thus, according to Allen and Fortin, these inter-species similarities in brain structure and processing support the idea that other mammal and bird species have a capacity for episodic memory.

Granting that humans actually do have a capacity for episodic memory, Allen and Fortin’s argument for the existence of episodic memory in other species is structured in just the way that I have argued the research program’s argument needs to be structured in order to support its claim that other species have a capacity for episodic memory. However, I do want to push their argument a bit, because although their approach to arguing for episodic memory in animals is effective, I do believe it warrants caution.

In one experiment that demonstrates inter-species similarity in the processing that underlies episodic memory, Allen et al. (2014) show that rats and humans perform similarly (in terms of reaction time, response pattern, and accuracy) on a task that involves memory of a specific sequence of events (presentation of distinct odors for the rat subjects and presentation of distinct images for the human subjects). They argue that their results suggest that humans and rats utilize similar cognitive processes and representations in remembering event sequences.¹³ Furthermore, because remembering the “flow of events” is an important aspect of human episodic memory, the authors argue that their study suggests that rats and humans share some of the mechanisms that are involved in episodic memory (specifically the mechanisms involved in remembering temporal ordering of events).

I believe this study is a step in the right direction towards showing that rats and humans have a kind of memory that works in the same way—it posits a specific hypothesis about how the data should look if rats and human memory of sequences of items work in similar ways. However, it brings us back to my earlier point that the way that episodic memory is defined matters. Simple sequencing of events might very well involve similar cognitive processes in humans and rats. However, this does not seem to mean that rats have episodic memory, unless we want to define episodic memory as memory for simple event sequences.¹⁴ This experiment thus might be evi-

¹³ Their strongest argument for the similarity of human and rat processing of the sequences comes from their “ordinal transfers” condition. In this condition, one item for one sequence (the X from WXYZ sequence, for example), would be transferred into the same ordinal position in a different learned sequence (X would replace the B in the sequence ABCD). The degree to which an ordinal transfer is judged to be out of sequence indicates the degree to which the subject represents the sequence using item-to-item associations versus using item-in-position associations. If the subject uses only item-to-item associations to remember the sequence, the argument goes, then the X in the sequence AXCD should always be judged to be out of sequence, since X should only ever follow W. If, however, sequences are coded in terms of the positions of their items, then the X in the sequence AXCD should not count as out of sequence. Allen et al.’s results suggest that both humans and rats utilize both item-to-item and item-in-position associations.

¹⁴ The authors do not claim that the rats’ performance in this study is evidence that they have episodic memory, but they do argue that their study suggests that this task can be used on rat models to study the underlying mechanisms of episodic memory. Furthermore, Allen et al. (2014) cite studies of rat memory for sequences as evidence that rats have a capacity for episodic memory.

dence that rats and humans have a similar-working capacity for episodic memory, but it depends on how we are defining episodic memory. The way that we describe the episodic memory phenomenon—and the way we describe the various memory phenomena that are studied under the episodic-like memory research program—makes a difference for the kinds of conclusions we can plausibly draw about the evolutionary continuity of episodic memory and the usefulness of animal models of episodic memory.

To see how the description of episodic memory matters, suppose we think it is best to think of episodic memory as a wide-spread phenomenon that is found in many different species. If this is the case, then it is likely that we will need to conceive of episodic memory as a broadly described phenomenon—something like memory for events in context (Allen and Fortin 2013)—so that it can describe behavior in many different species. Memory for events in context is broad enough that just what it amounts to can vary across species or models—for some it might involve memory of event sequences (like the rat example), for others it might involve remembering what–when–where information (like the scrub jay example)—and the situations in which this kind of memory are demonstrated may vary as well. The description of the episodic memory phenomenon is thus broad enough to include a variety of behaviors. The mechanisms that support this broadly described phenomenon are likely to involve a mixture of homologous and analogous structures and processes across species (Allen and Fortin 2013). These brain mechanisms might be similar in some ways—for example, they might occur within the same general brain regions (such as the hippocampus and the prefrontal cortex)—but they are likely to be only similar on some broad scale of comparison (like brain region), since “remembering events in context” can mean different things for different species.¹⁵ If this is the case, then we might think about episodic memory as a general function that can work, neurobiologically, in a number of different ways (though with some broader similarities).¹⁶ However, if this is the case, then using other species to model or study how human episodic memory works will not be a particularly fruitful endeavor, at least not without very careful consideration of the similarities and differences between the

¹⁵ For an example of a neural comparison that is too broad to really support the comparative psychological claim, take the argument that the hippocampus is an evolutionarily old structure, and since it is involved in human episodic memory, it would make sense, neurobiologically, that other animals with hippocampi have episodic memory as well (Salwiczek et al. 2010). Once the comparison of hippocampi becomes more fine-grained, this argument seems much less plausible. For example, although scrub-jays have a relatively large hippocampus compared to other bird species (Pravosudov and de Kort 2006), avian hippocampi do not receive higher-order, multimodally integrated information from the brain areas responsible for integrating sensory information (the neocortical association areas in mammals, and the dorsal ventricular ridge in birds) (Rattenborg and Gonzalez 2011). Given that reciprocal connections between neocortical association areas and the hippocampus are thought to play a crucial role in episodic memory encoding and retrieval in humans (Simons and Spiers 2003), the lack of such connections in scrub jays suggests that they cannot have an episodic memory system that works in a similar fashion as a human episodic memory system.

¹⁶ Clayton and Russell (2009) also argue for a broad conception of episodic memory, what they call a “perspectival memory trace”. Their definition is problematic for similar reasons: its breadth allows it to capture a variety of behaviors that are unlikely to all be served by similar neural mechanisms. Thus, it is detrimental to the overall goal of the research program.

human episodic memory system and the episodic memory system of the animal in question.¹⁷

Suppose, on the other hand, we are more precise in our description of the memory phenomena we are comparing across species. Returning to Allen et al.'s (2014) study of temporal sequence memory in rats discussed above, it seems as though rats and humans do indeed have a memory system that works in similar ways. Just what kind of memory system is this, however? One option is to describe this memory system as episodic, and conclude that rats and humans thus have episodic memory systems that work in similar ways. This is a broad description, and it carries with it some of the problems I discussed above. Remembering sequences of events might be a sub-capacity that is necessary for human episodic memory, and it might be supported by similar mechanisms in rats and humans, but this is not evidence that rats have a capacity for something like human episodic memory. Thus, another option is to describe this similar memory phenomenon more precisely as *memory for event sequences*. This description can be considered more precise because it captures the idea that memory of events sequences is a kind of sub-component of the episodic memory capacity (at least as episodic memory is discussed in Allen et al. 2014 and Allen and Fortin 2013).¹⁸ Describing the phenomenon as “episodic memory” is thus broader because episodic memory, on this conception of it, involves various processes, of which only one is memory of event sequences. By making the description of the memory system more fine-grained, we are making it more likely that the mechanisms will actually be similar: this experiment provides us with some evidence that rats and humans use similar mechanisms in remembering event sequences, but if we describe the memory phenomenon in this experiment more broadly as episodic memory and remembering event sequences is just one process involved in human episodic memory, then there are still many ways in which human episodic memory may work differently than rat episodic memory.¹⁹ Although we are no longer making exciting claims about nonhuman animals having episodic memory, this approach does leave us better able to make claims about the mechanistic similarities of specific memory processes across species.

One way of getting around the issue of episodic memory being too broadly described is by altering the operational definition of human episodic memory. For example, Cheng and Werning (2015) give a definition of episodic memory that is based on

¹⁷ And if such careful consideration is, in fact, required, then we probably do not really need the animal model, since we will already be required to know quite a bit about how human episodic memory works (see Steel's (2007) discussion of the “extrapolator's circle”).

¹⁸ Several authors seem to endorse the view that human episodic memory involves a variety of sub-processes (for example, Suddendorf and Corballis 2007; Tulving 2005).

¹⁹ My point here is inspired by Bechtel and Mundale's (1999) discussion of grains of explanation: there different degrees of precision we can use to describe both a phenomenon and the mechanisms that explain that phenomenon. None of these grains of explanations is the correct one; instead what matters is that the grain of description of the phenomenon matches the grain of description of the mechanisms that explain it. Given that the comparative program wants to be able to compare the mechanisms across species, the description of the mechanisms needs to be fine-grained enough to support good cross-species comparisons—the kind of comparisons that will allow us to determine if a particular species would make a good model for studying human memory disorders, for example. Thus, the description of the episodic memory phenomenon should be comparatively fine-grained.

the idea that the core of the episodic memory phenomenon is the representation of a temporal sequence of events that the subject experienced. Their definition is based in part on research that suggests the neural mechanisms for sequencing events are similar across different species. Thus, their definition allows us to rather easily fulfill the claim that other species have an episodic memory system that works, mechanistically, like the human episodic memory system. Note, however, that Cheng and Werning's definition is essentially a way of describing the episodic memory phenomenon in a more precise way. Thus, if we were to adopt Cheng and Werning's sequential analysis of episodic memory, and if we found evidence, as they suggest, that the storage of such sequentially experienced events are coded in similar ways in rat and human hippocampi, then we would have good reason to think rats have a similar capacity for episodic memory as Cheng and Werning define it, i.e. as representing and simulating a temporal sequence of events that was experienced by the subject. We would not, however, have evidence that rats have a capacity for some of the other phenomena, such as mental time travel, that often are either thought to define episodic memory or included as "part" of episodic memory. We would thus have good reason to use rats as models of this particular kind of memory. Of course, whether or not Cheng and Werning's sequential analysis of episodic memory is the "right" way to think about episodic memory is up for debate. My point in mentioning it is simply to show that their sequential analysis may be one way of constraining the phenomenon in such a way that the underlying mechanisms can be compared across species. What we want to avoid is having a definition of the phenomenon that is so broad that it allows for many different ways for it to work, neurobiologically. We have two ways of avoiding this: by either suitably precisifying the definition of episodic memory and keeping it consistent across models and species, or by breaking episodic memory up into various more specific memory processes that can be more easily operationalized and studied in other species.

We are thus left with the general question of how to define the episodic memory phenomenon for the comparative program. This is a difficult question that I do not intend to answer now, but I will give a few suggestions in light of what I have discussed here. First, I have argued that we need a definition that is fine-grained enough that it allows us to compare the neurobiological mechanisms that underlie the phenomenon, because this is the definition that will allow us to best serve the goals of the comparative program. Thus, the phenomenon should not be described so broadly that its definition allows for multiple different mechanisms to explain it.²⁰

The second suggestion has to do with the usefulness or plausibility of ascribing episodic-like memory to other species. I argued above that we should pay careful attention to the behaviors (and the capacities that underlie them) that an animal might use in the wild, rather than focus solely on the kinds of behaviors we can get these animals to do in the lab because we want to be able to claim that the animal has the

²⁰ By "multiple different mechanisms" I mean "multiple *very* different mechanisms"—assuming that both humans and nonhuman animals have episodic memory, we can always expect there to be some differences in the way the mechanisms underlying this phenomenon work, since there are, after all, species differences in the way brains are built. The differences simply should be small enough that they do not preclude the claim that the mechanisms work in the same way, and, importantly, the differences should not be so great that they change the way we characterize the episodic memory phenomenon across species.

capacity, rather than that the animal simply behaves as though it has the capacity. Thus, we want to make sure we are defining episodic memory in such a way that it reflects a capacity the animals actually have. However, we still want to make sure such a definition matches up with a particular human memory phenomenon, despite the fact that it is up for debate as to how best define this human memory phenomenon. One way we might be able both to give empirical support to the claim that episodic memory is an actual capacity animals have and use and to help define the human memory phenomenon by showing that using memory that is specifically episodic in nature actually improves task performance (in terms of, say, accuracy or efficiency) over simply using some other kind of memory or some other kind of information. That is to say, we want to be able to show that remembering something in an episodic way, as opposed to, say, a simple association, actually results in a differential performance on a task. This would bolster support for an explanation that includes an episodic-like memory capacity over an explanation that does not include such a capacity, since there would then be good reason to believe that the animals need some extra capacity to explain their performance. It would also help us define what episodic memory is, because it would single out the unique things episodic memory, specifically, does. Once we have a better idea of what episodic memory does for us we would be in a better position to say what processes are possibly involved.

7 Conclusion

Given that the goal of the episodic-like memory research program is to show that non-human animals have a capacity for episodic-like memory that works similar to human episodic memory, the claim that nonhuman animals possess episodic-like memory depends on three things: the definition of episodic memory in animals, the definition of episodic memory in humans, and a comparison of the mechanisms underlying the episodic memory capacity (however it ends up being defined) in each species. We need a definition of animal episodic memory that reflects a capacity that the animal actually uses in the wild, but also captures the essence of the human episodic memory phenomenon. We need a definition of human episodic memory that does not immediately preclude animals from having it and is clear enough to allow for a distinct mechanistic explanation. And we need both the human and animal definitions of the episodic memory phenomenon to be at a grain of description that allows for cross-species comparison of the mechanisms that explain the phenomenon, because this is how we will best support the claim that nonhuman animals have a capacity for episodic memory that works like the human capacity. These factors must work together in order to support a comparative claim about episodic memory. However, such an approach requires better mechanistic understanding of both human and animal memory, which, I have argued, has been hindered by the way that episodic-like memory has been operationally defined and studied.

Instead of attempting to find human-like memory systems within nonhuman animals, a better approach to studying animal memory may be to consider the unique features that memory systems of other species may have and how they relate to helping the species in its ecological niche. Episodic memory is not the best kind of memory for

all behaviors—other kinds of memory may be better suited for, say, seed caching and retrieval (indeed, it is hard to imagine humans being able to remember and recover thousands of cache sites without external aid). Perhaps the question should not be “is episodic memory uniquely human”, but rather “what kind of (potentially unique) memory system could support this particular species’ typical behavior in its natural environment?” Nonhuman animals might have memory systems that work in similar ways to human episodic memory, but they also might not—and it is not clear that basing the research program on making a comparison between human and animal behavior is the best way of discovering how animal (or human) memory works, for the reasons I have argued here.

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